

# Indian metoposaurid amphibians revised

DHURJATI PRASAD SENGUPTA

*Indian Statistical Institute, Geological Studies Unit 203 Barrackpore Trunk Road,  
Calcutta 700035, India (dhurjati@isical.ac.in)*

Received 18 August 2000; Revised manuscript accepted 30 November 2001

**Abstract.** A recent collection of more than a hundred fossil bones belonging to at least six individuals of metoposaurids from the basal part of the Late Triassic, Maleri Formation of the Pranhita-Godavari valley, Gondwana succession, has helped to formulate new ideas. Detailed morphological studies have been used to include all specimens of metoposaurids so far collected from India within a single taxon, *Buettneria maleriensis*, a new combination. A reconstruction of the skeleton of *Buettneria maleriensis* is presented for the first time. *Buettneria maleriensis* remains are common in the continental red beds of India, deposited under fluvial conditions witnessing seasonal climate changes. While some bones of *Buettneria maleriensis* were rolled and transported after death and are now found as sporadic fossils in mudstone (or occasionally in sandstones and calcirudites), the other type of occurrences, the rich accumulation of bones, are present only in mudstones. *Buettneria maleriensis* was replaced by the Chigutisauridae, a temnospondyl family exclusive to Gondwanaland. India is the only place where both metoposaurids and chigutisaurids are found in such close succession. The paleoposition of India during the later part of the Triassic may have been responsible for this.

**Key words:** *Buettneria*, India, Late Triassic, Maleri Formation

## Introduction

The Metoposauridae is a Late Triassic temnospondyl amphibian family known from Europe, North America, North Africa and India. They were quite large (at least 1.5 m in length), essentially aquatic animals (Defauw, 1989), with flat and heavily ornamented skull roofs marked with lateral line canals. Metoposaurids are to some extent morphologically similar to the present day crocodiles. However, unlike crocodiles, they had limbs unsuitable for quick movement on land.

The first metoposaurid, *Metoposaurus diagnosticus* (Meyer, 1842), was described from Europe. Subsequently a large number of metoposaurids belonging to several genera and species have also been reported from Europe and North America (Fraas, 1889, 1896, 1913; Lydekker, 1890; Watson, 1919; Romer, 1947; Colbert and Imbrie, 1956 and Werneburg, 1990). Dutuit (1976) carried out a study of another population of metoposaurids from North Africa. The Metoposauridae as a whole was extensively revised by Hunt (1993). However, Indian metoposaurids have not been studied in similar detail. Lydekker (1885) and Huene (1940) were the early workers to report metoposaurid fragments from India and Colbert (1958) discussed the significance of Indian metoposaurids in some detail. Later, Roychowdhury (1965) studied the Indian metoposaurids and recently a partial skull was described by Sengupta (1992).

A revision of the Indian metoposaurids has been attempted here in the light of the recovery of more than a hundred fossilised bones belonging to at least six individuals. These remains represent a mass accumulation and were found near Aigerapalli village in the basal part of the Maleri Formation of the Pranhita-Godavari valley of Central India.

Taphonomic and palaeobiogeographic studies of the metoposaurids have also revealed some interesting results. India is the only region where the typically Laurasian metoposaurs are found together with some stereospondyls exclusive to Gondwanaland. The significance of this association will be discussed.

## Family Metoposauridae

The family Metoposauridae is morphologically a very compact group which shares a number of character states. They have flat elongate skulls with tapering snouts, dorsolateral and anteriorly placed orbits, a pineal foramen far posterior to the orbits, low skulls with occipital condyles placed in the same line and plane (or a little posterior in certain cases) as the quadrate condyles, large paraquadrate foramina, spoollike intercentra (Romer, 1947; Watson, 1919, 1962; Colbert and Imbrie, 1956; Rouchowdhury, 1965; Dutuit, 1976) and wide cultriform process of the parasphenoid (Coldiron, 1978). In addition, Milner

(1990) noted that the palatine ramus of the pterygoid is rather short with a posteromedial ramus of the ectopterygoid contributing to the strut. Jupp and Warren (1986) stated that, in metoposaurids, the posterior coronoid forms part of the dorsal margin of the posterior Meckelian foramen. Warren and Snell (1991) further noted that the ilium of the metoposaurids has some taxonomic importance since the iliac blade is not "expanded" like other temnospondyls. They also noted that the metoposaurid humerus has well developed ends and prominent areas for muscle insertion, a rare trait among the temnospondyls. Both Werneburg (1990) and Warren and Snell (1991) suggested that the interclavicles of the metoposaurids have some characteristic features.

While the monophyly of the family Metoposauridae is established, the taxonomy at the generic level is somewhat problematic. There are only a few character states which are variable between different populations as well as within the single population of a particular area. The problem of taxonomy of metoposaurids at the generic level thus depends on proper understanding of those limited numbers of character states.

Colbert and Imbrie (1956) used two character states to differentiate the North American from the European populations. In the North American populations the lachrymal enters the orbit margin while in the European forms it does not. The degree of overlap of the clavicles on the interclavicles and the pattern of ornamentation of the clavicles were also different in the North American and European metoposaurids.

Roychowdhury (1965) grouped all the metoposaurid genera into a single genus, *Metoposaurus*. Subsequently Dutuit (1976) erected some new species from North Africa and designated them as *Metoposaurus* at the generic level. Gregory (1980) pointed out that there are at least two metoposaurid genera present in North America; one with an otic notch and the other without. Davidow-Henry (1989) divided the metoposaurids into three generic groups, one with otic notches, one without, and a third having a pineal foramen placed more forward than in the others. This splitting was continued by the recent work on metoposaurid taxonomy by Hunt (1993) and Milner (1994). Hunt (1993) divided the metoposaurids into five genera and six species. They are: *Metoposaurus diagnosticus* (Meyer, 1842), *M. bakeri* (Case, 1931), *Buettneria perfecta* (Case, 1922), *Dutuitosaurus ouazzoui* (Dutuit, 1976, new combination *sensu* Hunt, 1973), *Arganasaurus lyazidi* (Dutuit, 1976, new combination *sensu* Hunt, 1973) and *Apachesaurus gregorii* (Hunt, 1993). Hunt stated that the last-mentioned genus has a very shallow otic notch while in the other genera they are deeper.

The most conspicuous change in the work of Hunt (1993) is the lumping of many taxa found from various

places of the world into *Buettneria perfecta*, which also includes the Indian metoposaurid, *Metoposaurus maleriensis* (Roychowdhury, 1965), making it a junior synonym of *B. perfecta*. All the species of *Buettneria* have their lachrymals included within the border of the orbits.

Following a different approach, Milner (1994) grouped the metoposaurids into more than one "grade" which are further divided into certain "clades." He included "*M. maleriensis*" within the clade *Anaschisma*. The latter according to him is a "terminal clade" with the elongate lachrymal entering the orbit margin (a character-state of grade *Buettneria*), large, closely spaced nares and the supraorbital lateral line canals always broken behind the orbits (character states which separate *Anaschisma* from *Buettneria*).

### Indian metoposaurids

The history of the work on Indian metoposaurids was discussed in detail by Roychowdhury (1965). Only one more specimen of the family has been described in recent years by Sengupta (1992). Hence only a brief discussion on the Indian metoposaurids is provided below.

In India metoposaurids are known from the Maleri Formation of the Pranhita Godavari (P-G) valley and the Tiki Formation of the Son Mahanadi valley. Initially, the Indian metoposaurids were known from fragmentary surface collections which did not permit diagnosis below family level (Lydekker, 1885; Huene, 1940). Later, systematic collection of *in situ* specimens from the Maleri Formation yielded a number of well preserved fragments. These fragments were sufficiently diagnostic and included at least two partial skulls, clavicles and interclavicles, and vertebral elements. Roychowdhury (1965) erected *Metoposaurus maleriensis* on the basis of these specimens and also presented a restoration of the skull.

As mentioned earlier Hunt (1993) included *M. maleriensis* as *Buettneria perfecta*. The taxonomic status of the Indian metoposaurids is revised in the present work. All the specimens of the Indian metoposaurids are grouped into a single genus and species, *Buettneria maleriensis*, a new combination.

### Systematic paleontology

Order Temnospondyli Zittel, 1888  
Family Metoposauridae Watson, 1919  
Genus *Buettneria* Case, 1922

*Buettneria maleriensis* (Roychowdhury, 1965)  
new combination

Figures 1-16

*Metoposaurus maleriensis* Roychowdhury, 1965, p. 21, figs. 3-

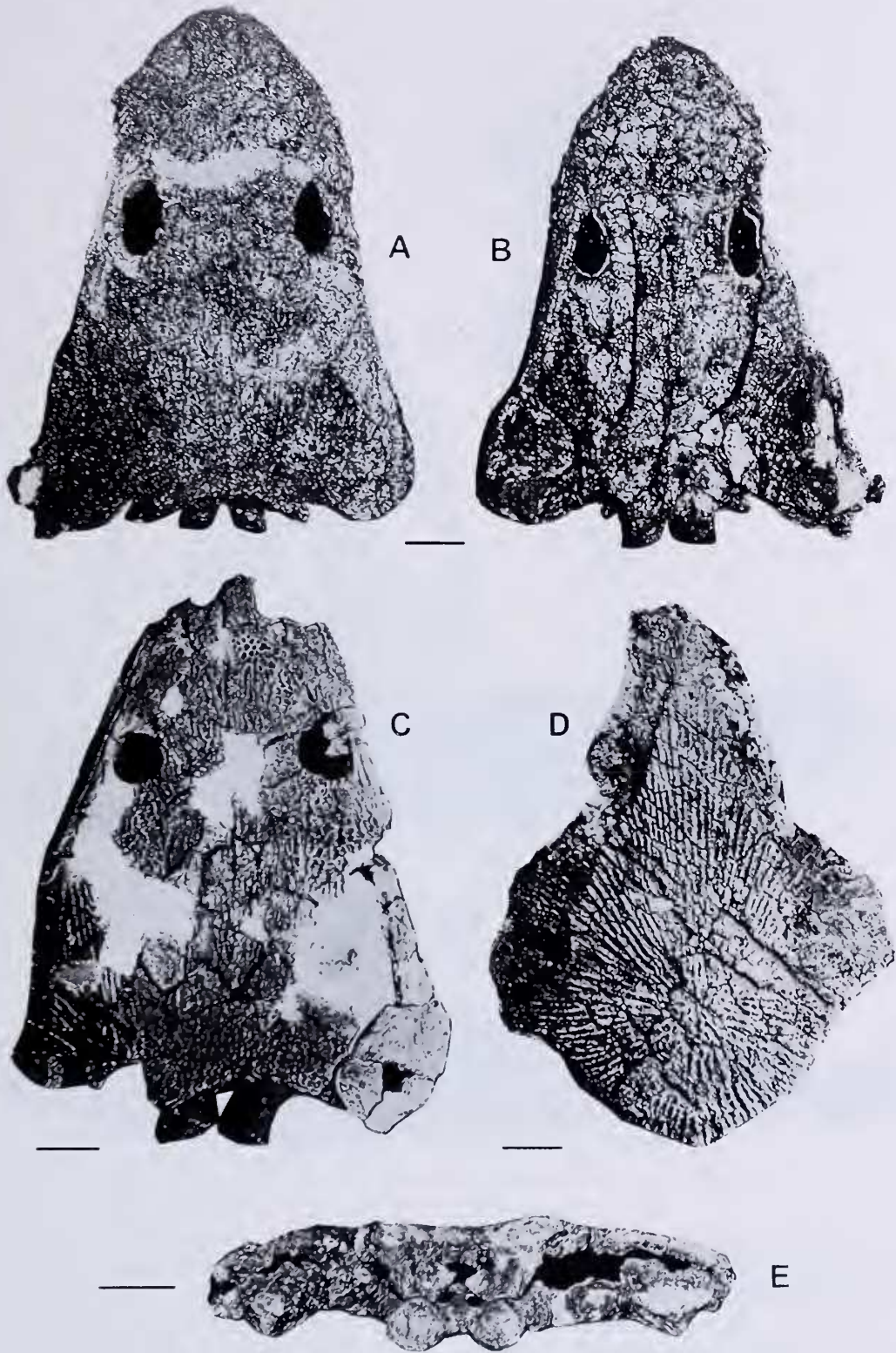
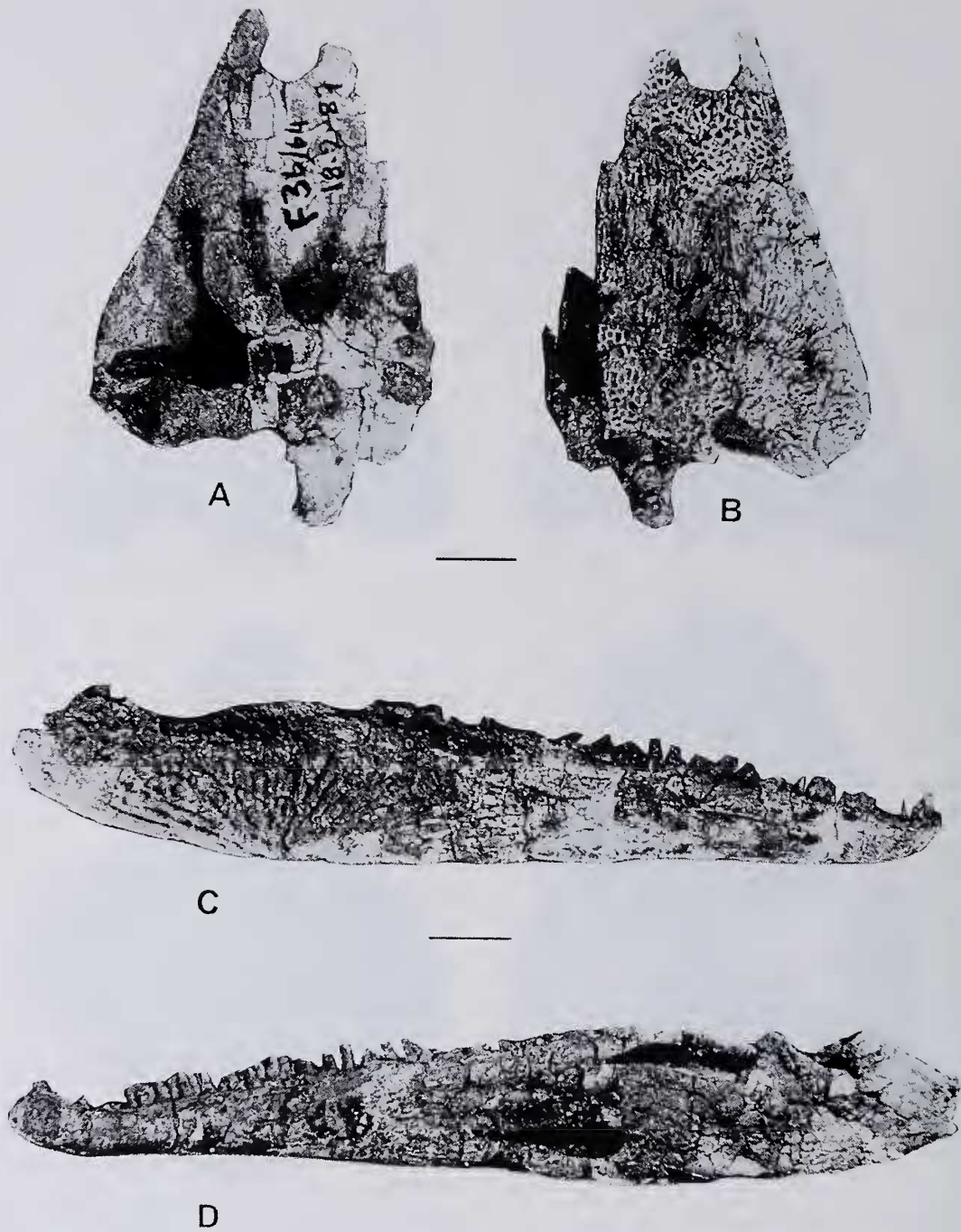
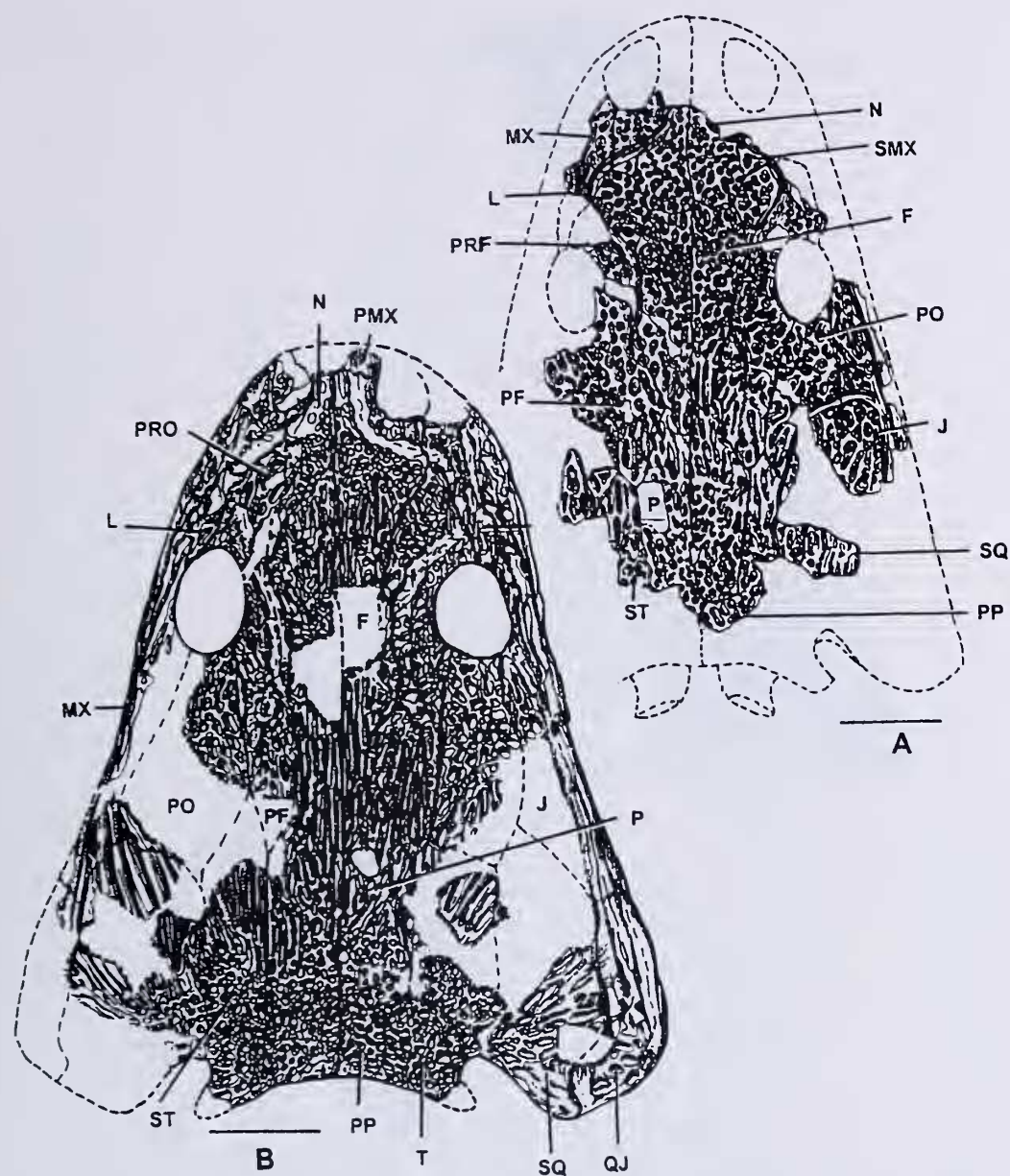


Figure 1. Skull roof (A = ISIA 56, C = ISIA 59), palate (B = ISIA 56), interclavicle (D = ISIA 67) and occiput (E = ISIA 53) of *Buettneria maleriensis*, new combination. Scale bars = 5 cm.



**Figure 2.** Palate (A = ISIA 58), skull roof (B = ISIA 58) and mandible (C, D = labial and lingual view of ISIA 60) of *Buettneria maleriensis*, new combination. Scale bars = 5cm.



**Figure 3.** Skull roof of *Buettneria maleriensis*, new combination. A = ISI A 4, B = ISI A 59. Abbreviations: F= frontal; J = jugal; L = lacrimal; N = nasal; P = parietal; PRF = prefrontal; PMX = premaxilla; PO = postorbital; PP = postparietal; PF = postfrontal; QJ = quadratojugal; SQ = squamosal; ST = supratemporal; T = tabular. Scale bars = 5 cm.

20, pls. 21–41; Sengupta, 1992, p. 300, figs. 1–4, pl. 1. *Buettneria perfecta*, Hunt, 1993, p. 78, figs. 7–9 (in part).

**Material examined.**—GSI 2249, 2254 and 2263 (Lydekker, 1885), K 33/638, 616a, b, 630a, 606a, 611a, 602a (Huene, 1940), ISI A 1 to 17 (Roychowdhury, 1965), ISI A 53 (Sengupta, 1992), ISI A 56, and ISI A 58 to 175. The specimens with numbers starting with ISI A are housed in the Geological Museum, Indian Statistical Institute, Calcutta,

India (Table 1) and specimens K 33/638, 616a, b, 630a, 606a, 611a, 602a, and GSI 2249, 2254 and 2263 are kept in the Indian Museum, Calcutta, India.

**Holotype.**—ISI A 4, in the collection of the Geology Museum, Indian Statistical Institute, Calcutta, India.

**Paratypes.**—ISI A 1 to 3 and ISI A 5 to 17, 53, 56, 58 to 175.

**Distribution and age.**—*B. maleriensis* occur in the lower part of the Maleri Formation of the Pranhita Godavari val-

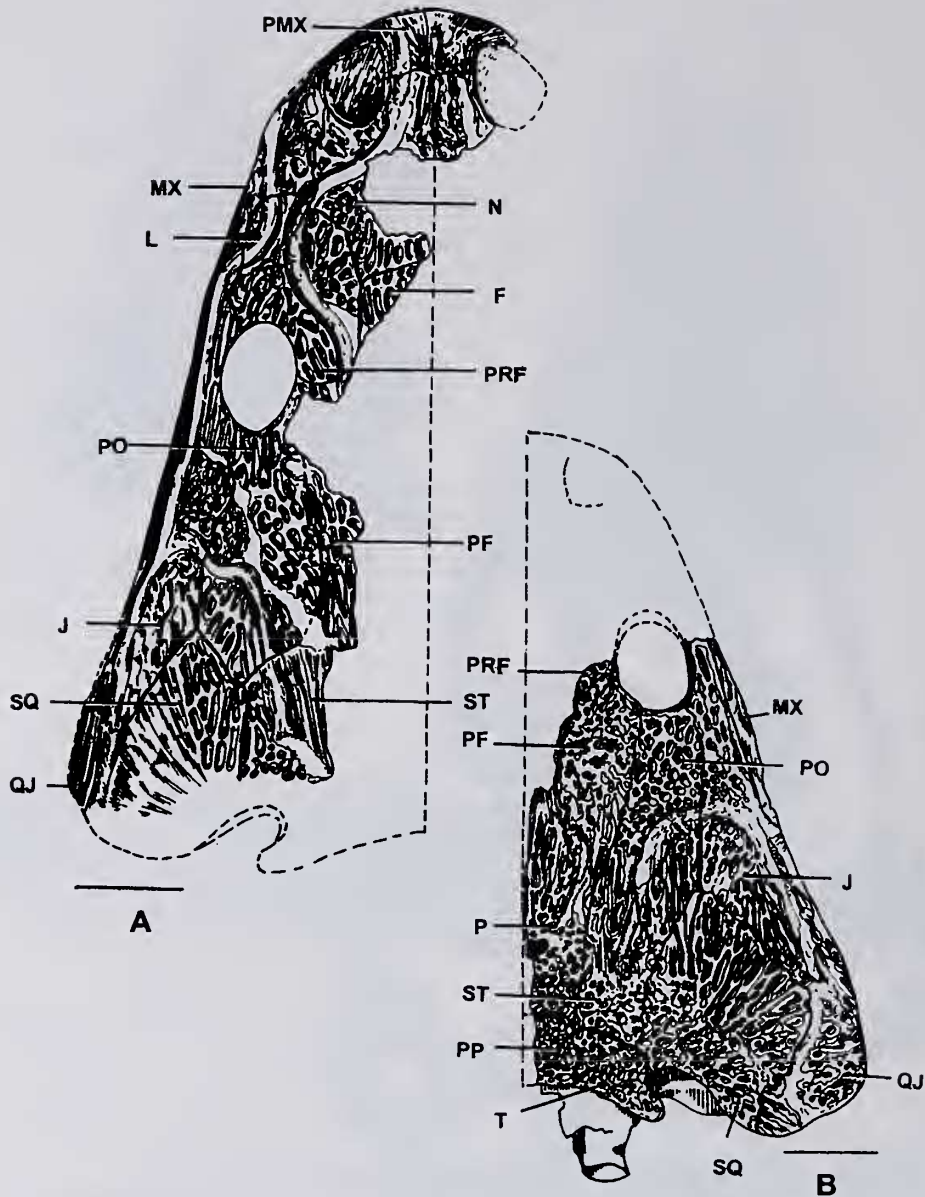


Figure 4. Skull roof of *Buettneria maleriensis*, new combination, A = ISI A 8, B = ISI A 58. Abbreviations used are same as Figure 3. Scale bars = 5 cm.

ley and also in the Tiki Formation of the Son Mahanadi valley of Central India. Material examined were mostly collected around the villages of Achlapur, Gampalpalli and Aiegarapalli, Adilabad District of Andhra Pradesh, India. The age of *B. maleriensis* is Late Carnian.

*Diagnostic characters.*—*Buettneria maleriensis* has the lachrymal in the margin of the orbits and thus it differs from all other metoposaurids except *B. perfecta*, *sensu* Hunt (1993). *B. maleriensis* differs from most specimens of *B. perfecta* in the presence of large, closely spaced nares and lateral line canals never forming a loop behind the or-

bits (Milner, 1994). Two specimens (FMNH UC 447 and 448, kept in the Field Museum of Natural History, University College collection, Chicago) designated as "*Anaschisma*" by Branson, 1905 have similarity with *B. maleriensis* in this regard. *B. maleriensis*, however, has a different type of ornament than that of "*Anaschisma*" and has a comparatively larger orbit.

The lachrymal is present as a narrow strip of bone in *B. maleriensis*. The anterior boundary of the lachrymal and that of the prefrontal are at the same level. All the specimens of *B. maleriensis* are unique in having parts of the

**Table 1.** List of the specimens of *Buettneria maleriensis* new combination, housed in the Geology Museum, Geological Studies Unit, Indian Statistical Institute (ISI) Calcutta.

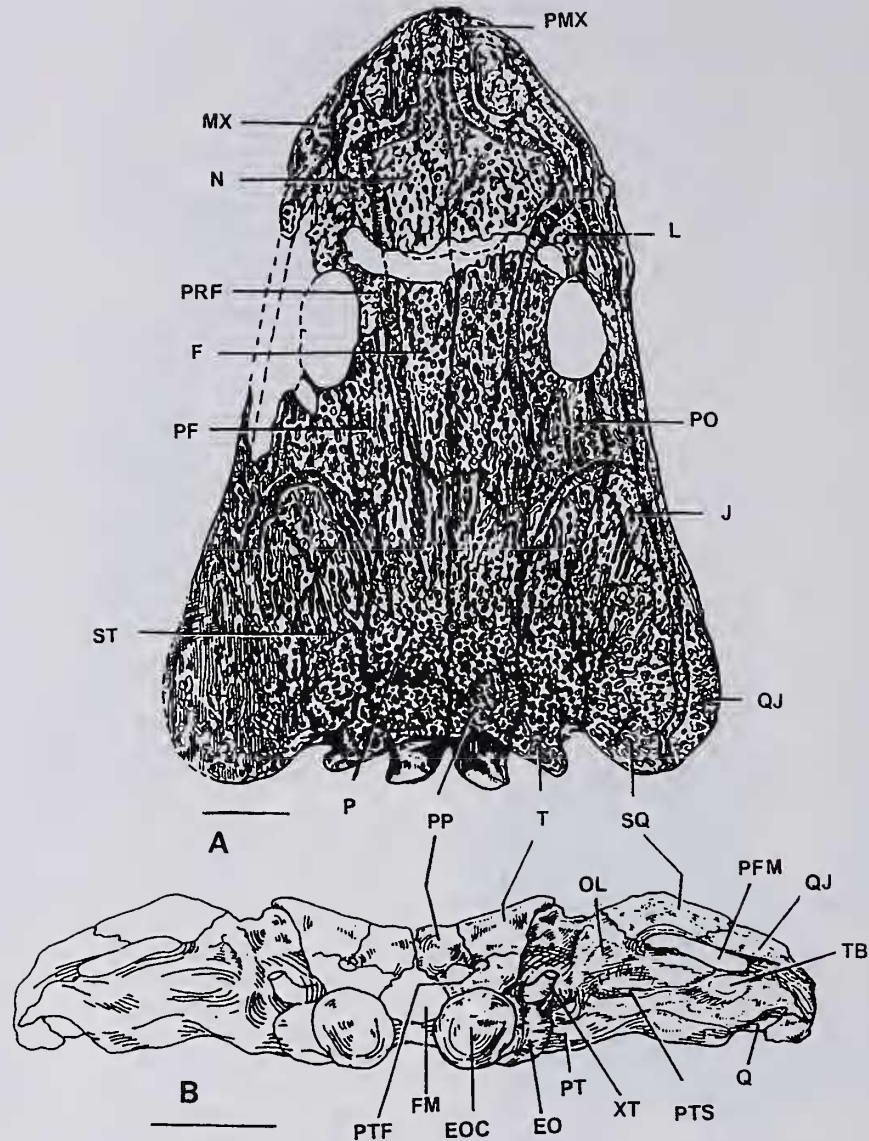
Element	ISI no.	Element	ISI no.	Element	ISI no.
Part of skull	ISI A 1	Femur, Right	ISI A 84	Intercentrum (Dorsal)	ISI A 129
Part of skull	ISI A 2	Femur, Right	ISI A 85	Intercentrum (Dorsal)	ISI A 130
Part of skull	ISI A 3	Ilium, Right	ISI A 86	Intercentrum (Dorsal)	ISI A 131
Part of skull	ISI A 4	Ilium, Right	ISI A 87	Intercentrum (Dorsal)	ISI A 132
Left squamosal	ISI A 5	Ilium, Right	ISI A 88	Intercentrum (Dorsal)	ISI A 133
Part of skull	ISI A 6	Scapulacoracoid, Rt	ISI A 89	Atlas	ISI A 134
Part of skull	ISI A 7	Scapulacoracoid, Rt	ISI A 90	Atlas	ISI A 135
Part of skull	ISI A 8	Scapulacoracoid, Rt	ISI A 91	Intercentrum (Caudal)	ISI A 136
Interclavicle	ISI A 9	Scapulacoracoid, Lt	ISI A 92	Intercentrum (Caudal)	ISI A 137
Left clavicle	ISI A 10	Scapulacoracoid, Lt	ISI A 93	Intercentrum (Caudal)	ISI A 138
Left clavicle	ISI A 11	Scapulacoracoid, Lt	ISI A 94	Intercentrum (Caudal)	ISI A 139
Right clavicle	ISI A 12	Ulna, Right	ISI A 95	Intercentrum (Caudal)	ISI A 140
Atlas	ISI A 13	Ulna, Right	ISI A 96	Intercentrum (Caudal)	ISI A 141
Four vertebrae	ISI A 14	Ulna, Left	ISI A 97	Intercentrum (Caudal)	ISI A 142
Three vertebrae	ISI A 15	Tibia, Right	ISI A 98	Intercentrum (Caudal)	ISI A 143
Right ischium	ISI A 16	Tibia, Left	ISI A 99	Intercentrum (Caudal)	ISI A 144
Left humerus	ISI A 17	Radius, Right	ISI A 100	Intercentrum (Caudal)	ISI A 145
Partial skull	ISI A 53	Fibula, Right	ISI A 101	Intercentrum (Caudal)	ISI A 146
Complete skull	ISI A 56	Neural spine	ISI A 102	Intercentrum (Caudal)	ISI A 147
Partial skull	ISI A 58	Neural spine	ISI A 103	Intercentrum (Caudal)	ISI A 148
Complete skull	ISI A 59	Neural spine	ISI A 104	Rib (Dorsal)	ISI A 149
Left msndible	ISI A 60	Neural spine	ISI A 105	Rib (Dorsal)	ISI A 150
Left mandible	ISI A 61	Intercentrum (Dorsal)	ISI A 106	Rib (Dorsal)	ISI A 151
Right mandible	ISI A 62	Intercentrum (Dorsal)	ISI A 107	Rib (Dorsal)	ISI A 152
Right mandible	ISI A 63	Intercentrum (Dorsal)	ISI A 108	Rib (Dorsal)	ISI A 153
Clavicle, left	ISI A 64	Intercentrum (Dorsal)	ISI A 109	Rib (Dorsal)	ISI A 154
Clavicle, left	ISI A 65	Intercentrum (Dorsal)	ISI A 110	Rib (Cervical)	ISI A 155
Interclavicle	ISI A 66	Intercentrum (Dorsal)	ISI A 111	Rib (Dorsal)	ISI A 156
Interclavicle	ISI A 67	Intercentrum (Dorsal)	ISI A 112	Rib (Dorsal)	ISI A 157
Humerus, Right	ISI A 68	Intercentrum (Dorsal)	ISI A 113	Rib (Dorsal)	ISI A 158
Humerus, Left	ISI A 69	Intercentrum (Dorsal)	ISI A 114	Rib (Dorsal)	ISI A 159
Humerus, Right	ISI A 70	Intercentrum (Dorsal)	ISI A 115	Rib (Caudal)	ISI A 160
Humerus, Right	ISI A 71	Intercentrum (Dorsal)	ISI A 116	Rib (Caudal)	ISI A 161
Humerus, Right	ISI A 72	Atlas with spine	ISI A 117	Rib (Dorsal)	ISI A 162
Humerus, Left	ISI A 73	Axis	ISI A 118	Rib (Dorsal)	ISI A 163
Humerus, Right	ISI A 74	Axis	ISI A 119	Rib (Cervical)	ISI A 164
Humerus, Right	ISI A 75	Axis	ISI A 120	Rib (Caudal)	ISI A 165
Humerus, Left	ISI A 76	Intercentrum (Dorsal)	ISI A 121	Rib (caudal)	ISI A 166
Ischium, Left	ISI A 77	Intercentrum (Dorsal)	ISI A 122	Phalange (post.right)	ISI A 167
Ischium, Right	ISI A 78	Intercentrum (Dorsal)	ISI A 123	Phalange (post.right)	ISI A 168
Ischium, Left	ISI A 79	Intercentrum (Dorsal)	ISI A 124	Phalange (post.right)	ISI A 169
Cleithrum, Left	ISI A 80	Intercentrum (Dorsal)	ISI A 125	Phalange (ant.right)	ISI A 170
Cleithrum, Right	ISI A 81	Intercentrum (Dorsal)	ISI A 126	Phalange (ant.right)	ISI A 171
Cleithrum, Left	ISI A 82	Intercentrum (Dorsal)	ISI A 127	Phalange (ant.right)	ISI A 172
Femur, Left	ISI A 83	Intercentrum (Dorsal)	ISI A 128	Phalange (ant.right)	ISI A 173
				Phalange (post.right)	ISI A 174

two main sets of the line canals, lateral and supraorbital, within the lachrymal. They are sinuous and touch each other inside the lachrymal.

The ratio of the width of the lachrymal at the orbit margin and the diameter of the orbit ranges between 0.2588 and 0.3409 in *B. maleriensis*. This ratio ranges from 0.6 to 0.4545 in case of *B. perfecta*. It appears that in *B. perfecta* the lachrymal is more equant and has a wider inser-

tion on the orbit margin (Case, 1922, fig. 1). This is evident also in "*B. howardensis*" (Sawin, 1945, fig. 3) and in "*Eupelor browni*" (Colbert and Imbrie, 1956, fig. 8) which were grouped into *B. perfecta* by Hunt (1993).

The curvature of otic notch, the shape of the tabular horn, the position and size of the orbits and the narial openings with respect to the skull length are also more uniform among the specimens of *B. maleriensis* than they are in *B.*



**Figure 5.** A = ISI A 56, skull roof of *Buettneria maleriensis*, new combination (abbreviations used are same as Figure 3). B = Occiput of *B. maleriensis*, based on the right side of ISIA 58. Abbreviations: EO = exoccipital; EOC = exoccipital condyle; FM = foramen magnum; OL = otic lamellae; PFM = paraquadrate foramen; PP = postparietal; PT = pterygoid; PTF = posttemporal fenestra; PTS = pterygoid sinus; Q = quadrate; QJ = quadratojugal; SQ = squamosal; XT = broken part of the stapes; T = tabular; TB = tubercule. Scale bars = 5 cm.

*perfecta*.

*Remarks.*—As discussed earlier, Hunt (1993) differentiated *Buettneria* from all other metoposaurids by the presence of the lachrymal in the orbit border. Other metoposaurids were further divided into several genera and species on the basis of certain synapomorphies and autapomorphies. For example, *Dutuitosaurus* and *Apachesaurus* share the apomorphy of having presacral centra with a diameter length < 0.8 cm and the former has the maxilla entering the orbit margin as an autapomorphy (Hunt 1993,

p. 80). For the genera which do not have the lachrymal in the orbit margin, the shape of the lachrymal was considered by Hunt (1993) to separate *Metoposaurus diagnosticus* from *Metoposaurus bakeri*. *Apachesaurus* has been partly characterised by the flexure of the supraorbital canal being separated from the lachrymal (Hunt, 1993, p. 81). However, all metoposaurids having their lachrymal in the orbit were grouped as *B. perfecta* by Hunt. The shape of the lachrymal or the position of the flexure of the supraorbital line canals or any other variations were not



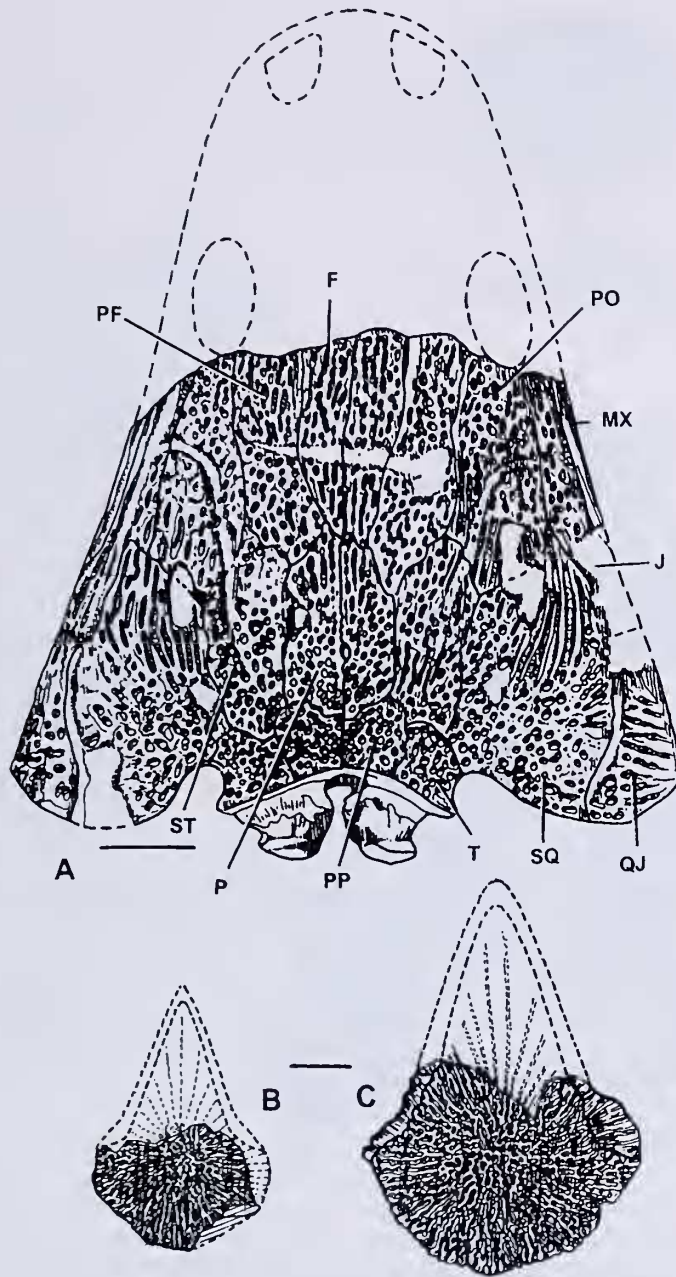
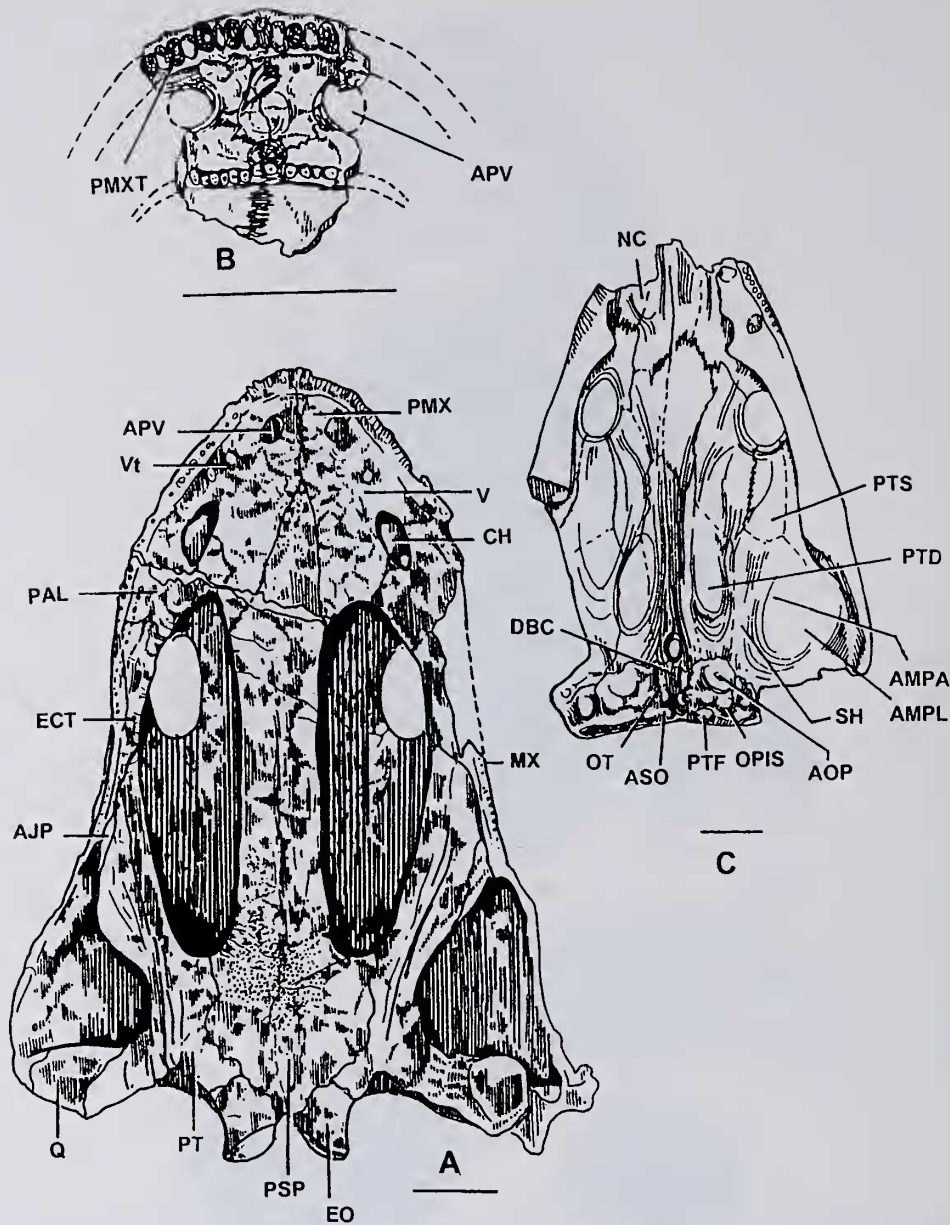


Figure 6. A = ISI A 53, skull roof of *Buettneria maleriensis*, new combination (abbreviations used are same as Figure 3). B, C = Interclavicles of *B. maleriensis*; B = collected from Tiki Formation (G.S.I. 2249, originally described by Lydekker 1885 as a skull roof bone), C = from Maleri (K33/638, Huene 1940). A, B and C are after Sengupta 1992. Scale bars = 5cm.

considered. Thus *Buettneria sensu* Hunt (1993) lacks any autapomorphy and results in a metataxon (Smith, 1994). Differentiating *B. maleriensis* from *B. perfecta* (*sensu* Hunt, 1993) on the basis of the width of the lachrymal at the orbit margin and the presence of the flexures of both the lateral and supraorbital line canals on the lachrymal is, therefore, relevant.

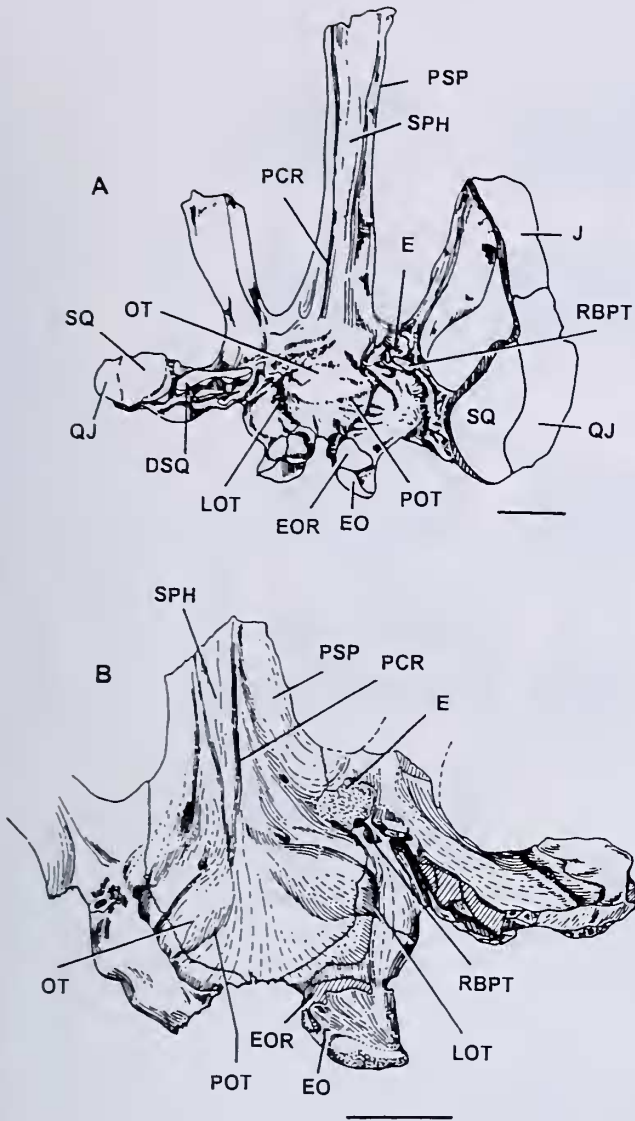
The localities yielding *B. perfecta* are restricted to the central and eastern United States, western Europe and northeastern Africa. During Late Triassic times these localities were believed to be very close and probably connected by land (Hunt, 1993, fig. 1). The population of *B. maleriensis* occurs outside that zone. Roychowdhury (1965) also emphasized the geographic isolation of the



**Figure 7.** A = ventral view of the palate of *Buettneria maleriensis*, new combination based on ISIA 56. B = the anterior palatal vacuities and the straight row of teeth behind based on a supplementary fragment ISIA 56a collected from Nalapur. Note the detached tooth, complete and well preserved, cemented later on the vomer. C = ventral view of the skull roof of *B. maleriensis* based on ISIA 59. Abbreviations: AJP = alar process of the jugal; AMPA = *adductor mandibulae*, posterior *articularis* (after Wilson, 1941); AMPL = *adductor mandibulae* posterior *longus* (after Wilson, 1941); AOP = attachment for the cartilaginous otic process; APV = anterior palatal vacuity; ASO = attachment for the supraoccipital; CH = choana; DBC = dorsal side of cartilaginous brain case; ECT = ectopterygoid; EO = exoccipital; MX = maxilla; NC = dorsal impression of the nasal capsule (after Wilson, 1941); OT = otic capsule; PAL = palatine; PMX = premaxilla; PMXT = premaxillary teeth; PSP = parasphenoid; PT = pterygoid; PTD = deep portion of *pterygoideus* (after Wilson, 1941); PTF = posttemporal fenestra; PTS = superficial *pterygoideus* (after Wilson, 1941); Q = quadrate; SH = *suspensorius hyoideus* (after Wilson, 1941); V = vomer; Vt = vomerine tusk. Scale bars = 5 cm.

Indian population and suggested that biometric studies could reveal its specific characters. The biometric studies of Indian metoposaurids will be dealt in a separate publication. Meanwhile certain observations are noted below.

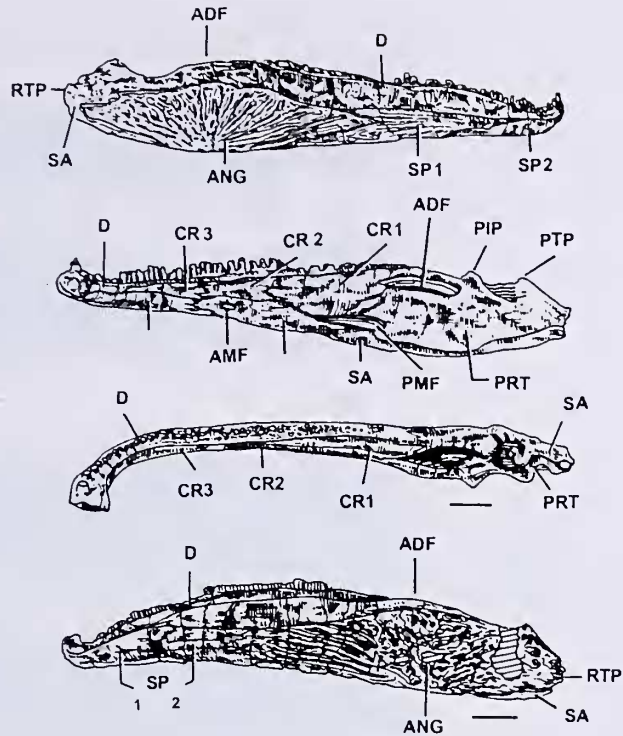
Colbert and Imbrie (1956, figs. 13, 14, p. 434-438, table 8) illustrated a technique to plot the bivariate population range diagram of certain skull roof parameters. The field range for *B. maleriensis* has been calculated using similar



**Figure 8.** Dorsal view of the palate of *Buettneria maleriensis*, new combination; **A** = ISI A 59; **B** = ISI A 7, after Roychowdhury (1965). Abbreviations: DSQ = descending process of the squamosal; E = epipterygoid; EO = exoccipital; EOR = ascending process of the exoccipital (broken); LOT = lateral ridge bounding otic region; OT = otic capsule; PCR = ridge on the cultriform process of the parasphenoid; POT = posterior ridge bounding otic region; PSP = parashenoid; QJ = quadratojugal; RBPT = rim of the basiptyergoid process; SPH = depression for sphenethmoid; SQ = squamosal. Scale bars = 5 cm. B.

techniques. It is found that the range of *B. maleriensis* is specific and only partly overlapping with the multigeneric North American species now grouped together as *Buettneria perfecta* by Hunt (1993).

Sengupta and Ghosh (1993) attempted some cephalometric studies of some of the individuals of the North American metoposaurids and *B. maleriensis*. They used several skull roof parameters and extracted three major



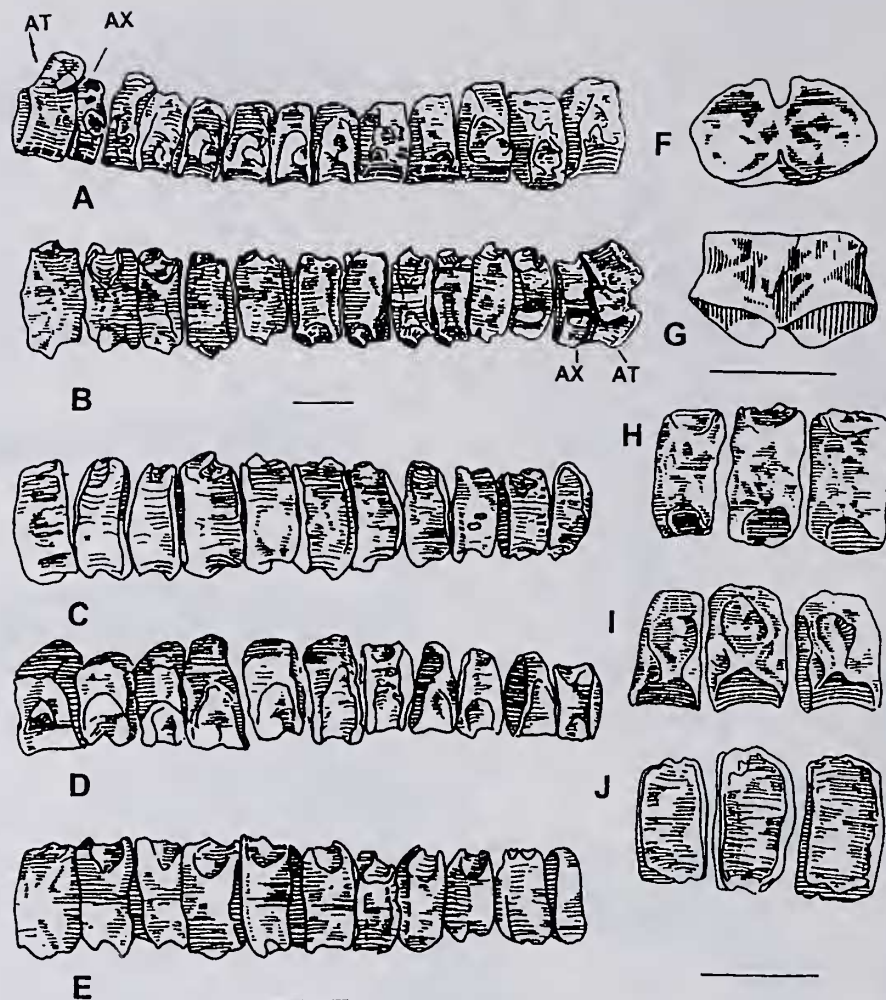
**Figure 9.** Right mandible of *Buettneria maleriensis*, new combination based on ISIA 60. From top: labial, lingual and dorsal views. Bottom: left mandible of *Buettneria maleriensis* based on ISIA 61. Abbreviations: ADF = adductor fossa; AMF = anterior Meckelian foramen; ANG = angular; CR (1,2,3) = coronoids; D = dentary; PIP = preglenoidal internal process; PMF = posterior Meckelian foramen; PRT = prearticular; PTP = postglenoidal process; RTP = retroarticular process; SA = surangular; SP (1,2) = splenials. Scale bar = 5 cm.

factors through a principal-component-based factor analysis. They found that the plots of the factor scores on two-dimensional Cartesian coordinates (Sengupta and Ghosh, 1993, fig. 2) indicate a peripheral position of the Indian metoposaurids with respect to the main concentration of the similar plots of the American metoposaurids.

**General characters of *Buettneria maleriensis***

Osteology of both the dorsal and ventral sides of the skull roof and of the palate of the metoposaurids have been described in some detail by Cope (1868), Fraas (1889, 1913), Case (1922, 1932), Watson (1919), Sawin (1945), Romer (1947), Colbert and Imbrie (1956), Roychowdhury (1965), Dutuit (1976) and Hunt (1993) among others. Wilson (1941) discussed the soft parts. Hence only the general characters of the skull of *B. maleriensis* are given below.

*Skull roof.*—*Buettneria maleriensis* has a very flat skull with short snout and anterolaterally placed orbits (Figures



**Figure 10.** Elements of vertebral columns of *Buettneria maleriensis*, new combination. A = lateral and B = dorsal views of one possible presacral column; C = dorsal, D = lateral and E = ventral views of second such pre sacral column. AT and AX are the atlas and the axis. Another single atlas with anterior (F) and dorsal (G) views are also shown. H, I and J are the dorsal, lateral and ventral views of a set of three adjacent caudal intercentra. All the specimens were collected from the Aigerapalli accumulation. Scale bars = 5 cm.

1A-C; 2A, B; 3; 4; 5A; 6A). Skulls have well defined, curved tabular horns and deep otic notches. The pineal foramen is placed well posterior to the orbit. The postparietal is shorter than the parietal.

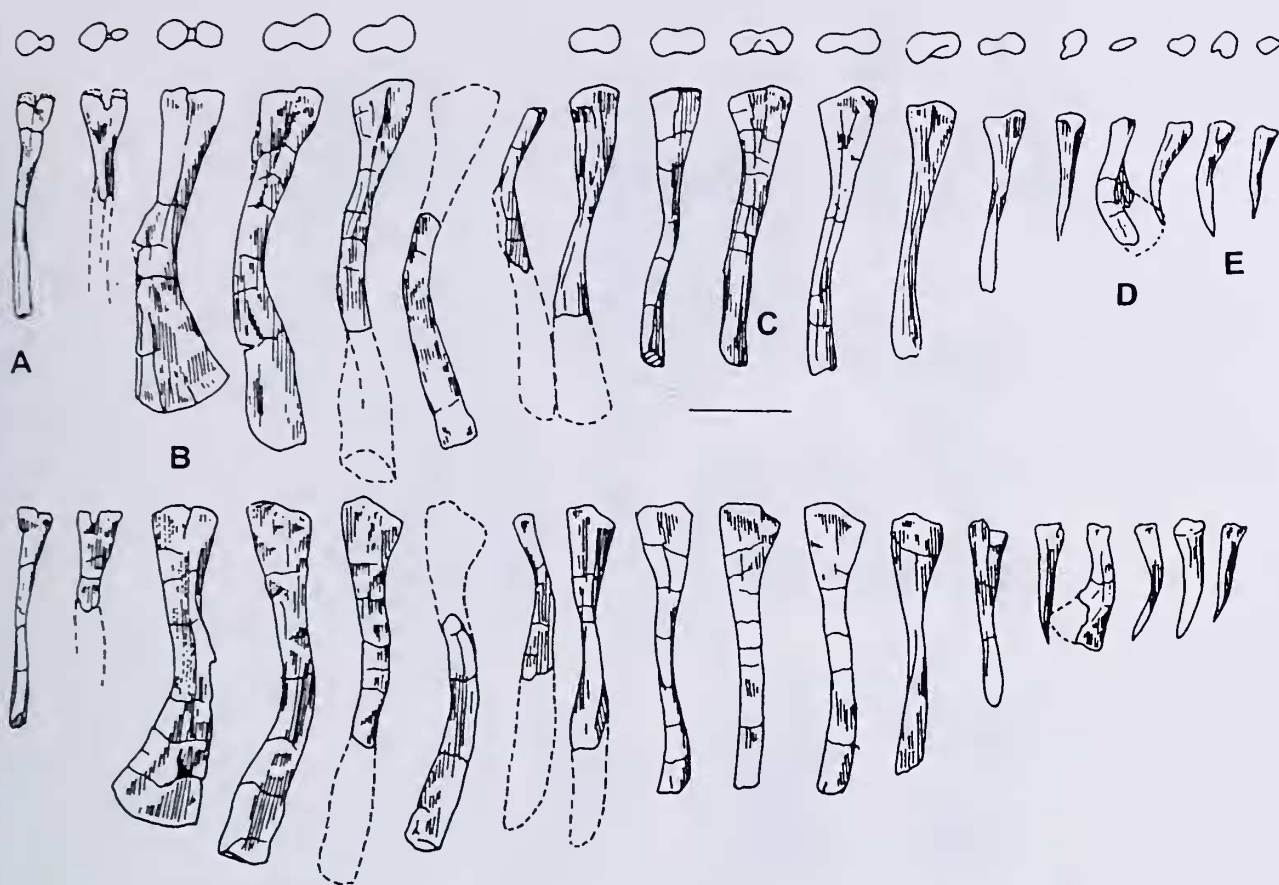
The posterior part of the skull has rather thick rectangular bones, namely the tabular, postparietal, parietal and supratemporal, which are strongly ornamented with circular pits walled by high ridges.

The snout, with close, large nares, is also well built with a similar type of ornament. Premaxilla and nasal are the two major bones in this area. Roychowdhury (1965) noted the presence of an extra bone in one of the specimens (ISI A 4) of *B. maleriensis* exposed on the dorsal surface of the skull. No such bone has been identified in any of the newly collected specimens. This is probably the extra

sutural growth noted in many temnospondyls (Romer, 1947; Welles and Cosgriff, 1965). The floor of the naris is made up of the septomaxilla which is thin and flat.

The middle part of the skull table is flat, thin and has elongate bones, namely, the frontal, postorbital, prefrontal and jugal with elongate ridges and valleys as ornament. The lateral line canals do not form a loop posterior to the orbit. The lachrymal becomes narrow and touches the orbit margin.

*Palate.*—The ventral side of the palate (Figure 7A, B) has a flat rectangular base composed of parasphenoid from which a triradiating structure emerges with two palatine rami of the pterygoid between sub temporal and interpterygoid vacuities and a wide, flat cultriform process of the parasphenoid in the middle. The latter connects the base



**Figure 11.** Ribs (left side) of *Buettneria maleriensis*, new combination based on specimens ISIA 149 to ISIA 166. The total number of cervical, thoracic, sacral and caudal ribs are not known. In the diagram, only the preserved specimens are arranged one after another (external view at the top and internal view at the bottom). A = one of the two cervical ribs preserved. B = a typical anterior thoracic rib; C = posterior thoracic rib; D = possibly the lone sacral rib and E = caudal rib. Scale bar = 5 cm.

of the parasphenoid to the wide vomers. On the ventral side of the skull roof a narrow ridge is present in the midline particularly in the postorbital part (Figure 7C). This tapers towards the anterior and is perforated by the pineal foramen. This ridge corresponds in position to the depression present on the dorsal side of the cultriform process of the parasphenoid. This depression probably housed the cartilaginous sphenethmoid (Figure 8).

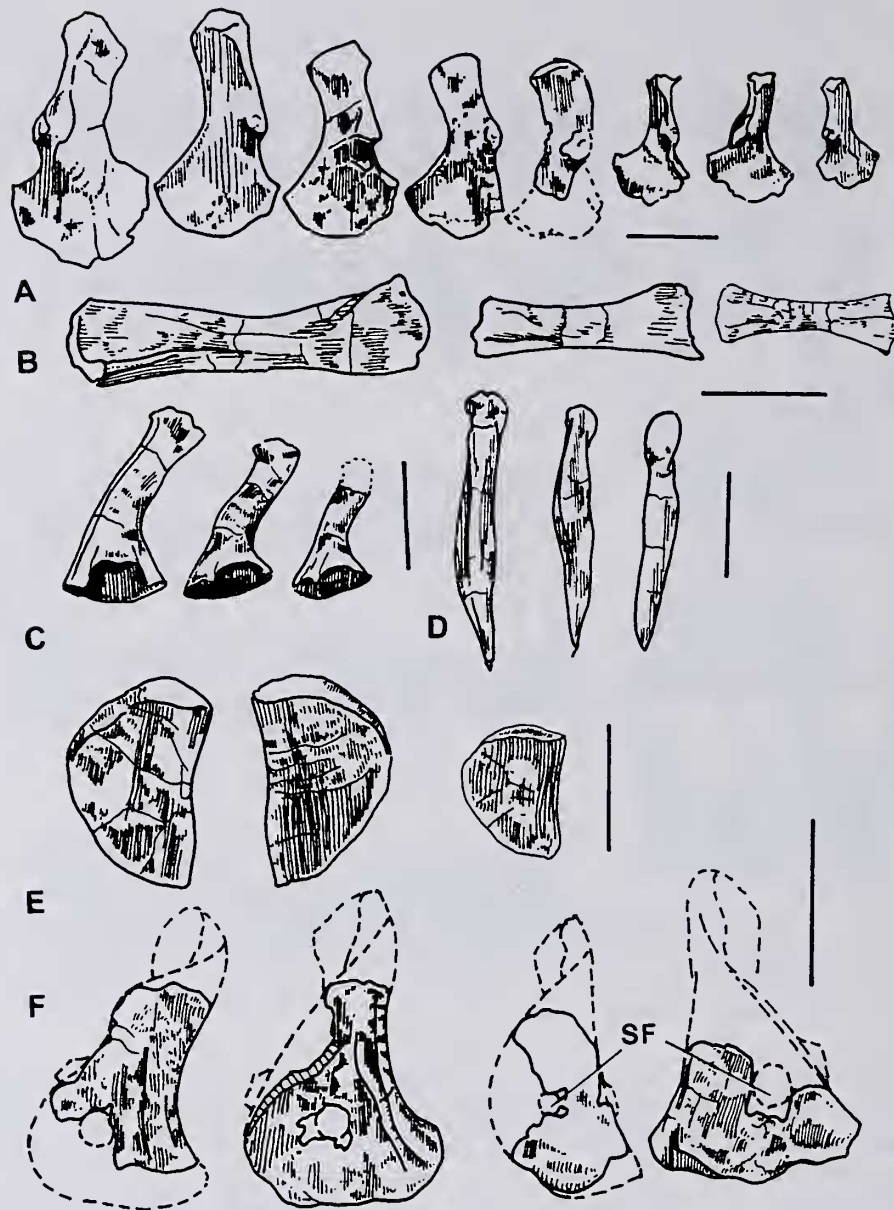
The position of the epipterygoid and the foramen of the internal carotids, the recess for the basiptyergoid process, the anterior end of the depression for the sphenethmoids and the position of the arcuate ridges bordering the otic region on the dorsal side of the palate of *B. maleriensis* are figured (Figure 8). These features, however, are similar in all the metoposaurids (see Case, 1922, figs. 2, 3; Wilson, 1941, figs. 1, 2; Roychowdhury, 1965, fig. 12; DuTuit, 1976, pls. 11–15).

On the dorsal side of the pterygoid, in ISI A 59, a part of the epipterygoid is preserved (Figure 8A, B). The ascend-

ing process of the epipterygoid was previously illustrated by Roychowdhury (1965, p 28). The braincase and associated features, the position of the epipterygoids and adjacent canals shown by Roychowdhury (1965), Case (1922) and DuTuit (1976) are noted in almost all the new specimens of *B. maleriensis*. Similar braincases are partly preserved in ISI A 7 and ISI A 59. The stapes is partly preserved in two individuals, ISI A 56 and ISI A 58 (Figure 5B).

*Maxillary and palatal dentitions.*—Maxillary and palatal dentitions extend far posterior to the centre of the interpterygoid vacuities. Vomerine and palatine tusks are present. One of the paratypes (ISI A 56a) has two well developed, circular, well separated, anterior palatal vacuities and a series of small vomerine teeth posterior to them (Figure 7A, B).

*Occiput.*—The occiput has the shape of a triangle with the base made up of postparietal and tabular on the dorsal side (Figure 5B). The exoccipital sutures with the postparietal and tabular housing a small, circular posttem-

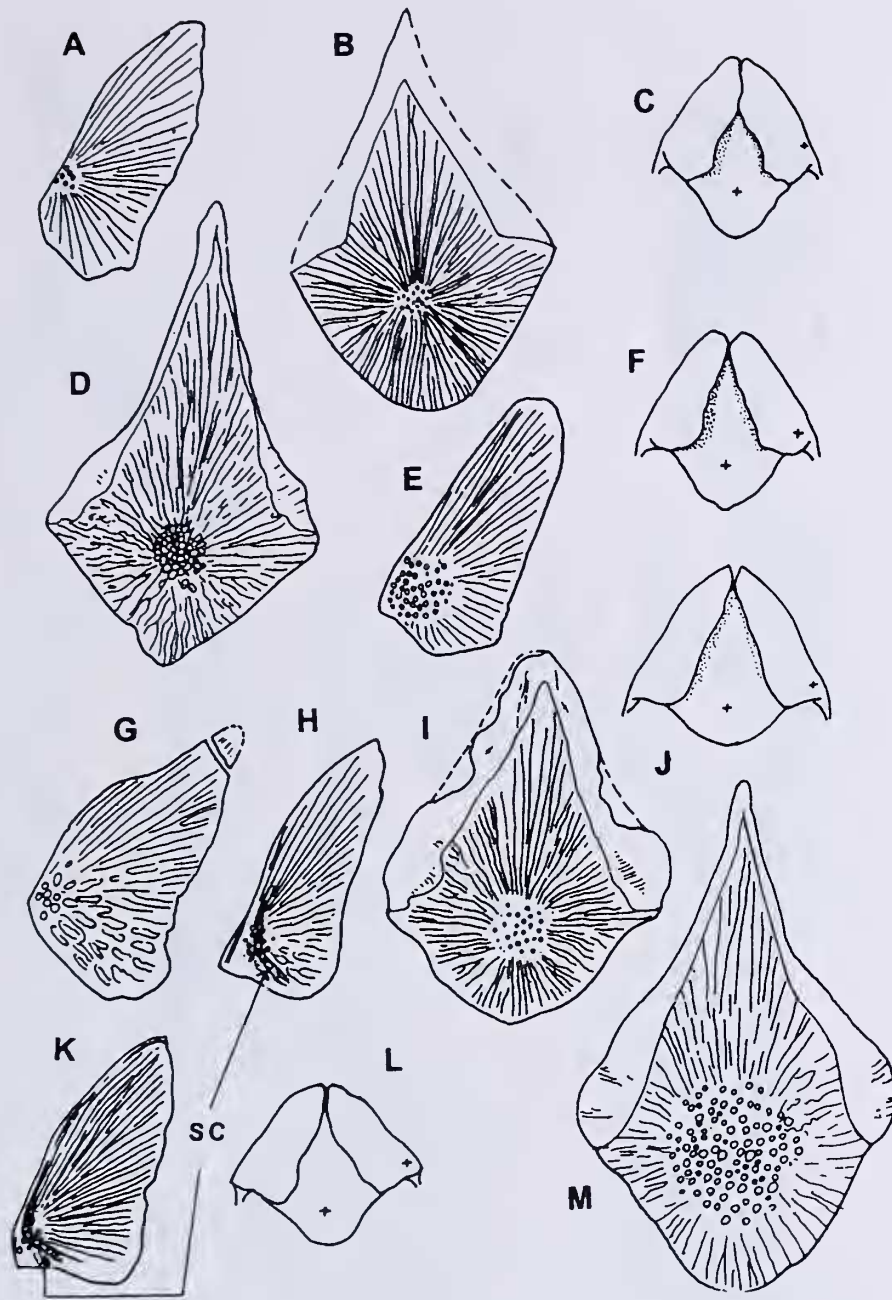


**Figure 12.** Some of the postcranial bones of *Buettneria maleriensis*, new combination, collected from the Aigerapalli metoposaur graveyard. A = Humeri, ventral view (ISIA 69 to 76), B = Femora, ventral view (ISIA 83 to 85), C = Ilii, lateral view (ISIA 86 to 88), D = Cleithra, mesial view (ISIA 80 to 82), E = Ischia, dorsal view (ISIA 77 to 79) and F = Scapulocoracoids, mesial view (ISIA 89, 90, 92, 94) with supraglenoid foramen (SF). Scale bars = 5 cm.

poral fossa at the junction of the three bones. The foramen magnum is at the centre of the triangle which is terminated by the flat parasphenoid and occipital condyles almost at the same ventral level. There is a little vaulting of the pterygoid and the ascending processes of the bone sutures with the quadratojugal and squamosal. These bones form the dorsal margin of a large, elliptical paraquadrate foramen. Unlike the earlier composite reconstruction of the occiput (Roychowdhury, 1965, fig. 11, p. 21), the speci-

mens described here show a thin insertion of the pterygoid in the lateral part of the paraquadrate foramen.

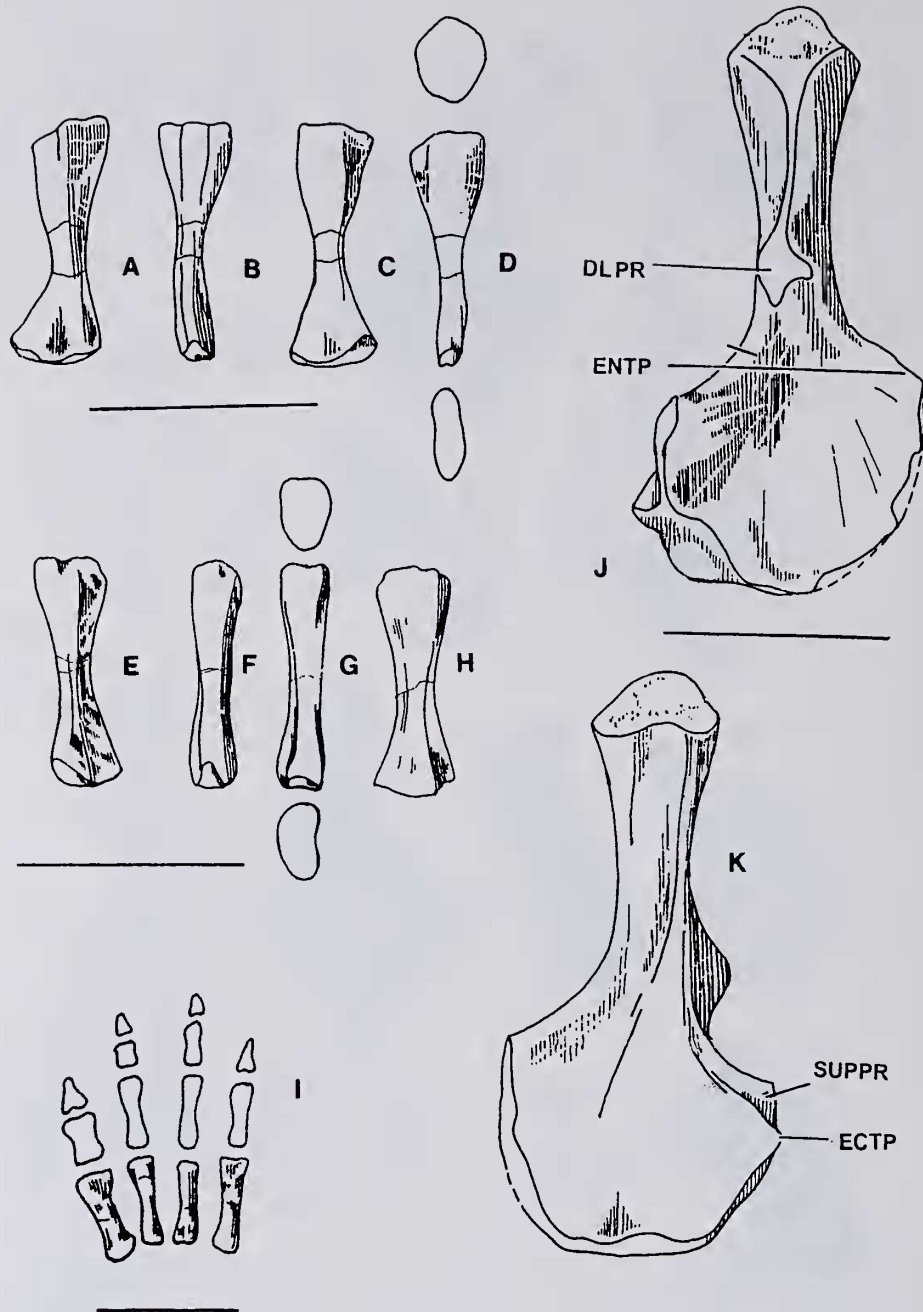
**Mandible.**—The mandible of *B. maleriensis* is described here for the first time. Two complete mandibles and a few broken fragments are available for study (Figure 9). The specimens are deepest in the region of the angular and their cross-sections are squared at the midlength. One of the specimens (ISIA 60) is more cylindrical in cross-section and narrow at the region of the spenials. The mandible has



**Figure 13.** Clavicles and interclavicles of *Metoposaurus diagnosticus* Fraas, 1913 (A = clavicle; B= interclavicle; C= clavicle interclavicle together); "*Buettneria howardensis*" Sawin, 1945 (D =clavicle; E = interclavicle; F = clavicle interclavicle together); *B. maliensis*, new combination, (G = clavicle; H = clavicle; I = interclavicle; J = clavicle interclavicle together); "*M. ouazzouri*" Dutuit, 1976 (K = clavicle; L= clavicle interclavicle together; M = interclavicle); Sc = sensory canal. For *B. maliensis* two different types of clavicles are shown (G and H). C; F and L are after Wernerburg (1990). Diagrams are schematic (not in scale) as interclavicles are enlarged (compared to respective clavicles) to illustrate the ornament.

a short retroarticular process with articular, surangular and prearticular exposed on the dorsal surface. Jupp and Warren (1986) described this as the type of postglenoid area noted in some temnospondyls including metopo-

saurids. The angular is the dominant bone of the labial side. On the lingual side a large, elongate posterior Meckelian foramen is present whose anterior border is formed by the posterior coronoid. The adductor fossa is



**Figure 14.** Right radius of *Buettneria maleriensis*, new combination, A = external, B = anterior, C = internal, D = posterior views and right ulna E = external, F = anterior, G = internal, H = posterior views (based on ISIA 100 and ISIA 95 respectively). I = digits of manus of the right side (ISI A 170, to 173, phalangeal formula based on Dutuit, 1976). Right humerus based on ISIA 68; J = Ventral, K = Dorsal views. DLPR = Deltoidal process; ECTP = ectepicondyle; ENTP = entepicondyle; SUPPR = supinator process. Scale bars = 5cm.

large and elliptical. No coronoid process is present. There is a large circular depression around the symphyseal tusk which forms part of the dentary tooth row. A small row of teeth is present on the inner side of the circular depression.

*Vertebral elements.*—All metoposaurids have typical discoid intercentra of different sizes and shapes (Figure 10). The overall shapes vary from circular to triangular and sometimes these variations are associated with their position in the vertebral column. Variations are also noted



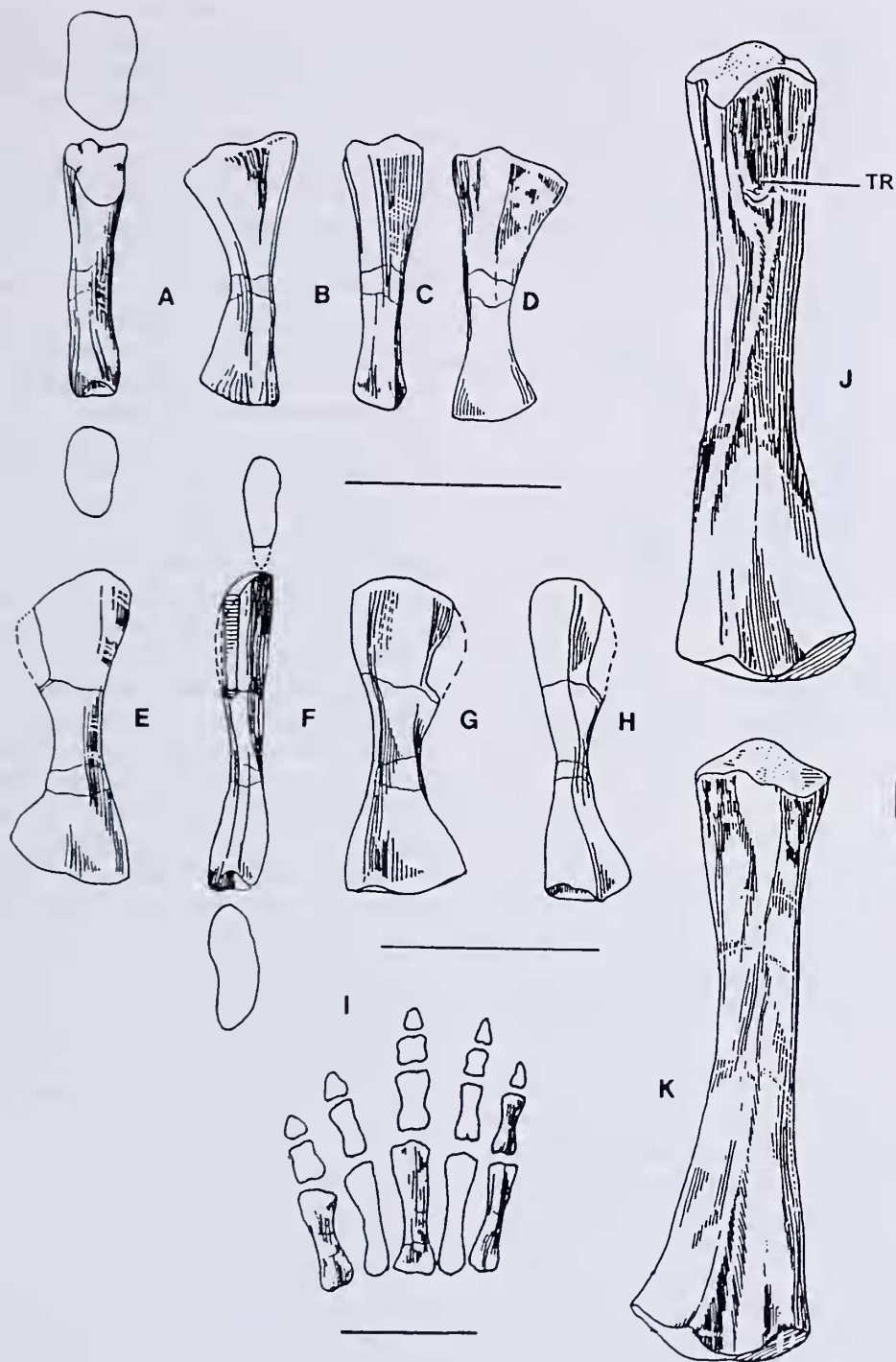
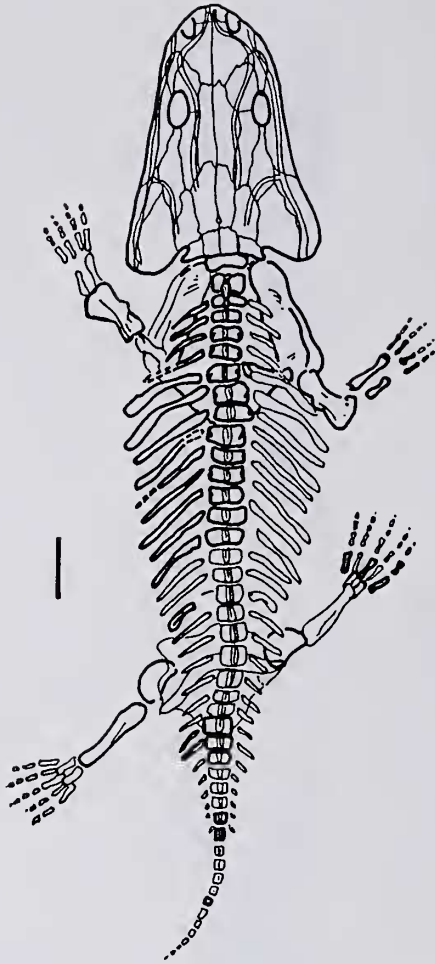


Figure 15. Left tibia of *Buettneria maleriensis*, new combination, A = posterior, B = internal, C = anterior, D = external and right fibula, E = posterior, F = internal, G = anterior, H = external. (based on ISIA 99 and 101 respectively). Pes of the right side (based on ISI A 167, 168, 169 and 174). Phalangeal formula based on Dutuit (1976). Left femur based on ISIA 83; J = ventral, K = dorsal views; TR = trochanter. Scale bars = 5 cm.

among individuals. The vertebral count of an individual of the metoposaurids is uncertain. Sawin (1945) figured 18 presacral intercentra for *Buettneria*. Dutuit (1976) illus-

trated 22 intercentra for one individual of "*M. ouazzoui*" (XIII /14/66) and 20 for another (XIII /4/66). In the reconstruction of *B. maleriensis* an average of 20 presacral



**Figure 16.** Composite restoration of *Buettneria maleriensis*, new combination. Dark lines represent elements from one individual. Scale bar = 10cm.

intercentra have been figured. The new collection from Aigerapalli includes 23 dorsal and 13 caudal intercentra. From the accumulation of vertebral elements of at least six individuals, parts of two possible columns (Figure 10) are reconstructed from the presacral vertebrae following Sawin (1945) and Dutuit (1976).

The atlas is double faceted at the anterior end to host the double condyles (Figure 10A, B, F, G). In one of the two inferred vertebral columns just mentioned (Figure 10A) the axis and one intercentra (possibly occurring just behind the axis) have two rib facets on the lateral side. In some of the intercentra the facets protrude whereas in larger intercentra (which are possibly further down the trunk), the posterior presacrals have only the facet without the neck. Anterior to the facet there is another curvature. In lateral view these two curvatures form an hourglass-like depression. This is more pronounced in the caudal intercentra (Figure

10I). The caudals are triangular in outline, quite flat on the dorsal side, platycoelous to opisthocoelous and smaller in size (Figure 10H–J). Sawin (1945) figured a sacral intercentrum which really differs little from some of the presacrals of the Indian taxon.

In one axis, a space created by the underside of the base of the posteriorly depressed neural arch and the scooped posterior dorsolateral part of the intercentrum clearly indicates the shape of the pleurocentrum. In another specimen, parts of the plerocentrum are preserved. Dutuit (1976) described one vertebra of "*M. ouazzoui*" where both the intercentrum and pleurocentrum are preserved and the combined centrum looks like a discoid with a slightly off-centered notochordal perforation. This type of vertebra has also been observed in *Compsocerops cosgriffi*, an Indian chigutisaurid (Sengupta, 1995). However, no such pleurocentral ossification is noted in *B. maleriensis*.

Unfortunately all the specimens in the collection have their neural arches broken. The axis has the base of the neural arch preserved in some specimens. An intervertebral position of the arches has been predicted by some authors (e.g. Roychowdhury, 1965; Dutuit, 1976; Warren and Snell, 1991). However, there is no direct evidence for this in the specimens of *B. maleriensis*.

**Ribs.**—The total number of ribs present is uncertain. Two cervical, several anterior presacral and some abdominal ribs have been found (Figure 11). One possible sacral and few caudal ribs are also present.

The cervicals have two separate facets or rib heads. The presacral rib heads are elliptical with capitulum and tuberculum connected by a narrow extension. The postsacral ribs have triangular or even squarish heads. The anterior presacral units have flattened distal extensions with unciniate processes. The abdominal ribs are cylindrical and lack the unciniate process. Warren and Snell (1991) noted that temnospondyls possess a single sacral rib which is expanded both proximally and distally and is stout and short. One short, curved and distally expanded rib is figured here as a possible sacral ribs (Figure 11D). It has a rather expanded proximal end but is quite thin. The caudals are shorter, curved and pointed distally.

**Elements of the pectoral girdle.**—The scapulocoracoid and the cleithrum are new additions to the Indian metoposaurid collections. They have the usual characters of metoposaurids (Dutuit, 1976). The clavicle and interclavicle have already been described (Roychowdhury, 1965). The scapulocoracoid has an enclosed supraglenoid opening (Figure 12F). This was considered as a primitive character (Warren and Snell, 1991). The cleithrum is spoon-shaped with dorsal expansions (Figure 12D).

**Clavicle and interclavicle.**—Roychowdhury (1965) noted two different types of clavicles in the Indian metoposaurids. He also mentioned that the clavicles of *M. diag-*

*nosticus* have a long contact anterior to the interclavicle which is not seen in *B. maleriensis*. Sengupta (1992) illustrated two similar-looking interclavicles, one from the Tiki and the other from the Maleri Formation which are redrawn here (Figures 6B, C). Colbert and Imbrie (1956) used the difference in the position of the centre of ossification and the variable nature of the clavicle-interclavicle overlap as taxonomically important characters. This variability was also highlighted by Warren and Snell (1991) and Werneburg (1990). Figure 13 indicates the clavicles and interclavicles of different metoposaurid taxa with variations in the ornament, position of the centre of ossification and nature of overlap of the clavicle on the interclavicle. However, ISI A 12 as illustrated by Roychowdhury (1965, figure 18), has a unique shape. A sensory canal is present in the clavicles of the Indian metoposaurids. This was also noted in *M. ouazzoui* (Dutuit, 1976).

*Ilium and ischium*.—The ischium is a semicircular bone and the ilium is elongate with a dorsal blade which is rather thick (Figure 12C). Warren and Snell (1991) considered this as a character of taxonomic value.

*Fore limbs*.—The humerus, like all other metoposaurid humeri, is well built, twisted and has pronounced processes for muscle attachments (Figure 14J, K). The ulna (Figure 14A–D) and radius (Figure 14E–H) are similar to the ones described by Dutuit (1976) for the metoposaurids from Morocco. Some digits of the right manus were also found (Figure 14I).

*Hind limbs*.—The femur, figured for the first time here (Figure 15J, K), is rather long and fully ossified with complete distal and proximal articular surfaces. The areas for *trochanters* are well developed. The tibia (Figure 15A–D), fibula (Figure 15E–H) and some digits of the right pes (Figure 15I) are also figured. The proximal and distal end of the tibia and fibula are less expanded than in "*B. howardensis*" as figured by Sawin (1945).

A composite restoration of *B. maleriensis* is shown in Figure 16.

### Aspects of taphonomy

*Buettneria maleriensis*, as stated earlier, is known from a large number of specimens from the Maleri Formation of the Pranhita-Godavari valley. Its occurrence in the Tiki Formation of the Son Mahanadi valley is rare. Hence emphasis is given here to the geology and the nature of occurrence of *B. maleriensis* in the Maleri Formation.

*Geological attributes*.—Mudstone, sandstone and peloidal calcarenite/calcirudite of various colours of the Maleri Formation crop out in NW-SE trending linear belts (Figure 17). The overall dip is 12 to 18 degrees towards the NE. The paleocurrent direction is towards the north.

The mudstone is dominantly red in colour and is structureless. Smectite is the major constituent of the clayey part (Sarkar, 1988). Haematite crystals are also common and iron oxide is responsible for the red colour (Robinson, 1970). The mudstones are exceptionally rich in vertebrate fossils. The sandstone is usually calcareous, cross-bedded, fine- to coarse-grained, containing weathered feldspars and infrequent garnets. Rock fragments and clay galls of different size, shape and colours are common. Fining-upward sequences are discernible in the sandstones (Sarkar, 1988). The sand bodies form narrow elongate ridges with mudstone valleys in between.

The peloidal calcarenite/calcirudite occurs either as solitary mounds and/or a string of such mounds within the red mudstone and also at the bottom of the sandstone (Sarkar, 1988, p. 267). The peloidal calcarenite/calcirudites are cross-bedded with overlapping troughs of various magnitudes and comprise calcite-cemented spherical or discoid peloids of micrite or microsparry calcite. According to Sarkar (1988) the paucity of broken abraded peloids and other evidences indicate a local pedogenic origin of the peloids.

Sengupta (1970) noted that while the mudstones represent the interchannel facies, the sand bodies are deposited in the channels of a meandering river system flowing north in a large valley trending NW-SE. Maulik and Chaudhuri (1983) described such sandbodies as ephemeral channel fills.

*Palaeoclimate*.—Pascoe (1959) suggested that the Maleri sediments were deposited in an extremely arid environment. Robinson (1970) first noted that the red mudstones of the Pranhita-Godavari valley were not necessarily deposited in desert like conditions. The Maleri vertebrate fauna indicates a well watered country. The colour of the mudstone is imparted by iron oxides and the high content of ferric oxides and presence of haematite crystals indicate an oxidising environment of deposition. Recent works suggest that the red colour may be remotely linked with climate (Pye, 1983). The absence of many desiccation cracks and footprints as well as the occurrence of fewer evaporites indicate that the climate was not arid. This is also supported by the presence of unionids and an array of aquatic or amphibious vertebrates. The paucity of plants was previously considered as an indicator of aridity. However, this is negative evidence and a good number of herbivore remains are found. On the other hand, the high smectite content (Sarkar, 1988) may indicate low rainfall (Singer, 1980). Peloidal calcirudite and arenite are also indicative of reworking of older soil profiles (Sarkar, 1988). To explain the contrasting evidence it is suggested that there was possibly seasonality in the climate. The aquatic members of the Maleri fauna, living in ephemeral rivers, had survived the drier situations by concentrating in the more permanent bodies of water (Robinson, 1971; Chatterjee *et al.*,

1987).

*Mode of occurrence.*—Animals living in the lowland habitat are mostly found in the floodplain deposits of the Maleri Formation (Kutty, 1971). Though exact proportions are difficult to determine, the number of lowland metoposaurids are always more than those of the robust rhynchosaurs and phytosaurs. The floodplains were well watered with a good drainage as remains of lowland or semiaquatic vertebrates are found there, associated with occasional bivalves, fossil wood and other sporadic plant debris, within thick red-coloured mudstones (Behrensmeyer and Hook, 1992).

Fossils are found as cracked, flaked or distorted bones which are often covered by peloidal calcirudite and calcarenite and calcareous concretions. Various stages of bone weathering (Behrensmeyer, 1982) are also present in the fossilized bones of the Pranhita-Godavari valley (Sengupta, 1990). The transported, disarticulated, abraded bones indicate large time gaps between their death and burial (Behrensmeyer and Hook, 1992)

In most of the red beds of the Maleri Formation vertebrate remains occur chiefly as surface accumulations of stray fragments and also as *in situ* bones in the floodplains. The *in situ* bones, in turn, can be fragmentary or complete. Four taphonomic facies can be identified in the Maleri sediments. The vertebrate bones occur as 1) complete *in situ* material in the mudstone, 2) fragmentary but *in situ* material in mudstone, 3) well preserved but broken bone accumulation in the sandbodies or in the peloids and 4) stray surface accumulation in the mudstones. Types 2 and 3 can be subdivided into i) isolated but broken skeletal parts and ii) fragments of one or more skeletal elements.

Bones belonging to metoposaurids are found in all these types of accumulations. Most of the metoposaurid material described by the early workers like Miall (1875), Lydekker (1885) and Huene (1940) belonged to taphonomic facies 4. Voorhies (1969) noted three major groups of bones according to their potential for dispersal particularly by water. The bulk of the specimens of *B. maleriensis* belong to Voorhies' (1969) group which constitutes an assemblage of skulls and mandibles. This indicates the transported nature of the metoposaurid material from the Maleri Formation. The most common skull fragments are of the tabular area as it is the strongest. The jaws are frequently represented by the symphyses. The skull margins are often preserved, without the thin midskull region. The deposition of peloidal calcirudites of diagenetic origin on the bones indicates various orders of reworking.

The above taphonomic picture indicates that, after death, the semiaquatic and lowland fauna of the Maleri Formation, living in a seasonal climate, were mostly exposed on the flood plains and were fragmented and transported (and even reworked). The lowermost mudstone

unit of the Maleri Formation is the thickest (Figure 17) and there the remains of lowland vertebrates are high in number. In that unit, due to some events leading to mass accumulations, finds like Aigerapalli came into being. A closer look at the Aigerapalli site may reveal some more information.

*Taphonomy of the Aigerapalli accumulation.*—The Aigerapalli site, near the base of the basal mudstone, chiefly comprises mudstones of red colour, with a few streaks of white, calcareous, fine- to medium-grained well-sorted sandstone. The bones were excavated from an area of only 10 m by 5 m which yielded over 100 disarticulated bones of several individuals.

There are 9 humeri (6 from the right side and 3 from the left) from six individuals with three different size ranges (Figure 12A). As indicated by the size ranges, two individuals were larger in size, one intermediate and three were small. The larger humeri come in the size range of 12.6 to 11.5 cm in length. There are three such specimens (a left and two from right) from two individuals. The next size range is a left and a right humerus of around 10 cm length possibly representing another individual. The last size range is around 6 cm length and from 4 specimens (three from left and one right) at least three individuals can be identified. The three size domains are also supported by the length of the three femora (Figure 12B). However, two skulls were recovered of which one is complete.

Though the thickest mudstone unit of the Maleri contains the metoposaur accumulation, sporadic occurrence of peloidal calcarenites/rudites within the unit suggests intermittent exposure to aridity. In fact, it is argued in the section dealing with paleoclimate that contradictory evidence for aridity and humidity are present in the lithology and fauna of the Maleri Formation and a seasonal climate could be a possible explanation. The aquatic fauna survived in small deeper pools at the time of aridity and might have moved away in search of safer places (Robinson, 1971, Chatterjee *et al.*, 1987). While doing so they could be trapped in the thick mud. Their remains were buried after being scattered by various agents. The bones have evidences of some amount of transportation. On the other hand, some of the small postcranial as well as a number of small and delicate teeth are well preserved. Hence, the transportation was possibly not prolonged.

The Aigerapalli type of bone accumulation is not uncommon at other metoposaurid-yielding localities around the world (Romer, 1939; Dutuit, 1976). The absence of articulated individuals is marked in the Aigerapalli and also in the mass accumulation of metoposaurids in the Lamy amphibian quarry in New Mexico (Romer, 1939). The latter has a similar taphonomic background to Aigerapalli where hydrodynamic sorting of bones of dead individuals from a residual pool affected by drought has been thought

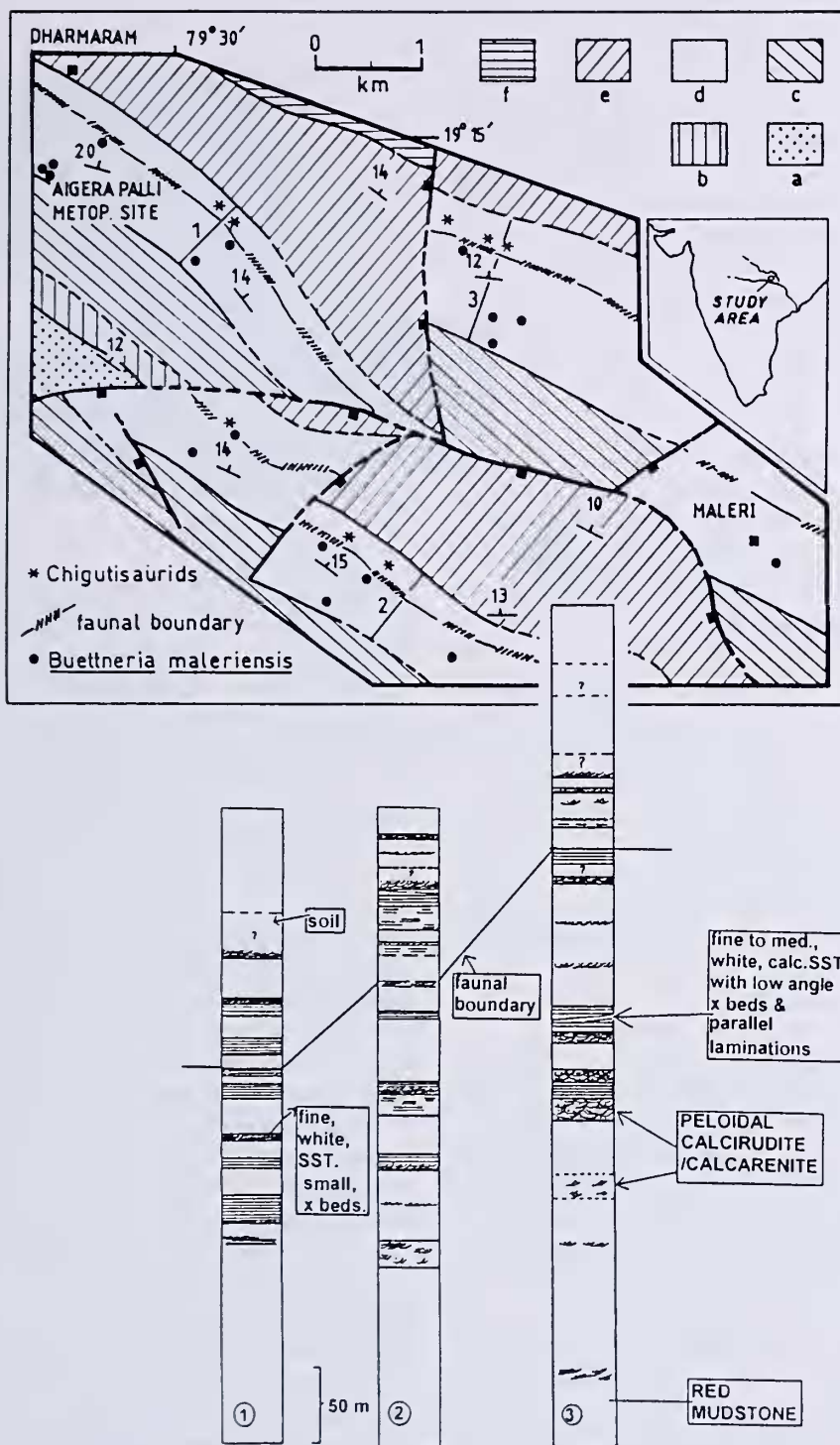


Figure 17. Geological map around the villages of Maleri and Dharmaram. Legends: a = Kamthi Formation, b = Yerrapalli Formation, c = Bhimaram Formation, d = Maleri Formation. Within the Maleri Formation the boundary between the lower and upper Maleri fauna is shown. The lines 1, 2 and 3 represent the positions of the columnar sections shown below the map.

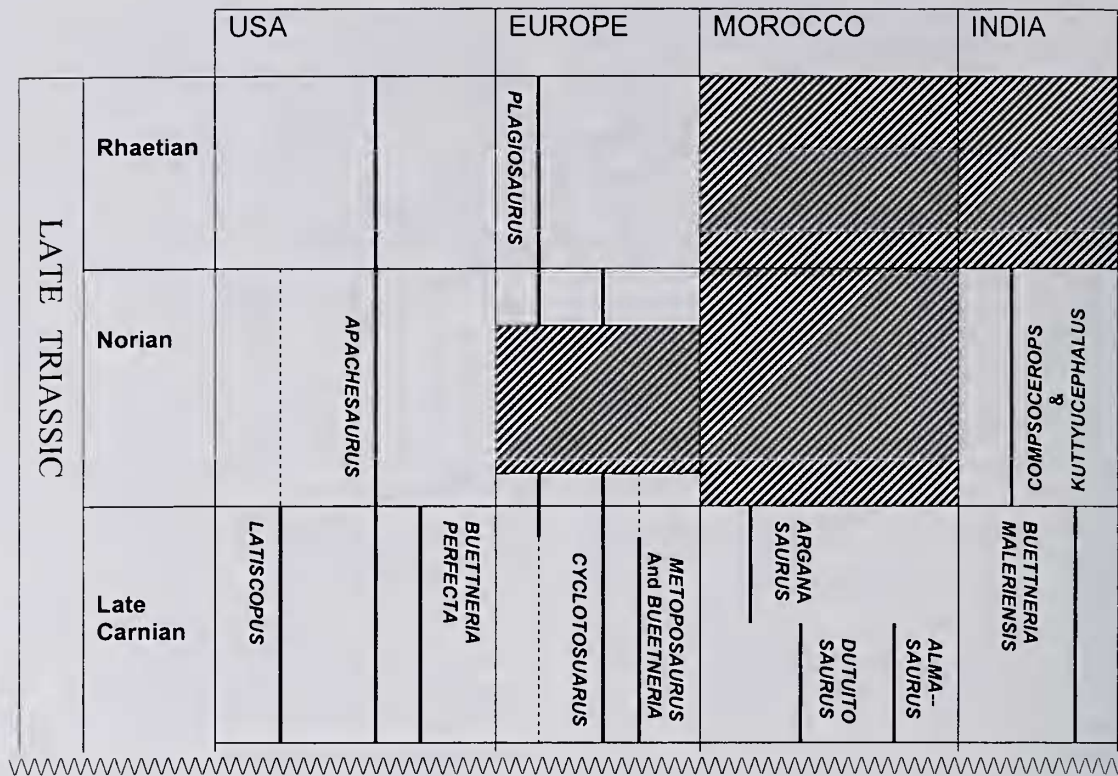


Figure 18. Stratigraphic ranges of metoposaurids and other associated temnospondyls of the Late Triassic Period.

to be the reason behind the accumulation (Romer, 1939; Hunt and Lucas, 1989)

#### Stratigraphic range of *B. maleriensis*

Roychowdhury (1965) suggested that the Maleri fauna is Carnian or early to middle Norian in age. Subsequently Kutty and Sengupta (1989) divided the Maleri fauna into two groups, a lower and an upper. The age of the lower group, which includes *B. maleriensis*, was stated as Late Carnian. The fauna associated with *B. maleriensis* chiefly consists of the phytosaur *Parasuchus* (*Paleorhinus*), the rhynchosaur *Paradapedon*, the theropod *Alwalkeria*, the protosaurus *Malerisaurus*, the cynodont *Exeraetodon*, an aetosaur and a large dicynodont. Hunt (1993), following the scheme of Lucas and Hunt (1989), put the lower Maleri fauna into the early part of the Late Carnian. The presence of *Paleorhinus* which is found from Tuvulian marine strata of Austria and stands as a good marker fossil in continental deposits, helped to infer this age (Hunt and Lucas, 1991).

Lucas (1998), stated that palynostratigraphy, sequence stratigraphy and magnetostratigraphy of the Chinle Group indicate a Late Carnian age and the principal correlatives are the lower Maleri, Schilfsandstein, Kieselsandstein, and

Blasensandstein of the German Keuper and the Argana fauna of Morocco. There is dispute also whether the lower Maleri fauna is early Late Carnian as stated by Hunt (1993) and Hunt and Lucas (1991) or late Late Carnian as stated by Kutty and Sengupta (1989). Hunt and Lucas (1991) predicted the age of the lower and upper Maleri faunas on the basis of phytosaurs. The Upper Maleri phytosaurs are yet to be described in detail. Moreover, immediately above the upper Maleri the Lower Dharmaram fauna (Kutty and Sengupta, 1989) also has an undescribed phytosaur and one or more aetosaurs. Bandyopadhyay and Roychowdhury (1996) noted that *Rutiodon*-like phytosaurs are found only from the upper Maleri and the age of the immediately overlying lower Dharmaram could be Late Norian. This suggests an Early Norian age for the upper Maleri fauna confirming the late Late Carnian age of the lower Maleri fauna occurring immediately below. Hence, it is likely that the last appearance datum of *B. maleriensis* is late Late Carnian.

Except in North America all metoposaurids were restricted to the Carnian. In North America, the Dockum Formation of Western Texas, Bull Canyon and Redonda Formations of Eastern New Mexico, the Painted Desert Member of the Petrified Forest Formation and the Owl

Rock Formation of northeastern Arizona have metoposaurids younger than Carnian in age. The post Carnian metoposaurid, *Apachesaurus*, is not abundant compared to the Carnian occurrences (Hunt, 1993). From the Southwestern United States, Long and Murry (1995) noted "a definite replacement of large metoposaurids by smaller ones" during the Early Norian. No small temnospondyls like *Apachesaurus* (Hunt, 1993) and *Laticopus* (Wilson, 1948) from North America or *Almasaurus* (Dutuit, 1976) from Morocco are found in the Late Triassic deposits of Europe or India. On the other hand, no brachyopid temnospondyl, with parabolic skull and deep palate with downturned pterygoids, has been described from the North American Late Triassic (Figure 18). Such temnospondyls are represented in Europe by the plagiosaurids (Kuhn, 1932; Milner, 1994) and in India by the chigutisaurids (Sengupta, 1995).

#### Paleoposition of India and aspects of paleogeography, paleoclimate and faunal migration

Metoposaurids are restricted chiefly to latitude 40 to 60 North, with the exceptions being the Indian occurrences. The distance of the latter from the other localities was, however, minimised to some extent by the union of the continents during the Late Triassic. On the other hand, chigutisaurids are thought to have originated in Australia (Warren and Hutchinson, 1983) and are so far found to be restricted to Gondwana. India is the only place where metoposaurids were replaced by the chigutisaurids. This has led to some interesting observations on the paleoposition of India and some aspects of paleoclimate, paleogeography and faunal migration.

The absence of endemism among the Late Triassic Indian tetrapods has long been known (Colbert, 1958; Chatterjee and Hotton, 1986). Cox (1974) noticed that the similarity coefficient of Indian fauna with that of North America and Europe is quite high (59% and 81% respectively). On the other hand that with Africa and South America is also not negligible (75% and 56%).

Smith and Briden (1977; map 13, p. 24) have shown that, during the Triassic, Australia was close to India and so were Europe and North America. The circum-Tethyan shoreline is short and curved and the position of Africa was such that the land distance between India and North America was minimal. The figures shown by Hay *et al.* (1982) indicate the position of India was almost halfway between North America and Australia at the end of the Triassic.

Cox (1974) noted that in the Triassic there were no major climatic barriers. Robinson (1973) postulated a sharply seasonal rainfall in parts of North America, Europe, Africa and India during the Triassic (Robinson, 1973, fig. 10).

Parrish *et al.* (1982, fig. 5, p. 39) have also shown that during Induan time a low pressure belt was located in Africa with an adjacent high in the north of India and another one in Europe causing a similar type of wind flow in the areas close to the Tethys. The entire area had 100 to 200 units of rainfall (Parrish *et al.*, 1982) without any major climatic barrier. The Late Triassic metoposaurids could have come from Laurasia along the circum-Tethyan shoreline to India as a geographically peripheral group (this could also support the contention that the Indian metoposaurid, *B. maleriensis*, is a distinct taxon). Chigutisaurids, on the other hand, arrived later, either from Australia or South America.

#### Acknowledgements

The work was part of the integrated research programme of the Pranhita -Godavari valley carried out by the Geological Studies Unit, Indian Statistical Institute, Calcutta. The field work was funded by the Institute. The specimens were collected by many workers of the Institute. T. Roychowdhury and T. S. Kutty collected and prepared many of the specimens and so did D. Pradhan and Shiladri Das of the Geological Studies Unit (GSU). I am thankful to T. Roychowdhury for critically going through the manuscript. A. Warren of La Trobe University, Victoria reviewed the manuscript and helped to improve it. She and A. Milner of Birkbeck College, London, also helped in recognizing certain taxonomically important characters of the metoposaurids.

#### References

- Bandyopadhyay, S. and Roychowdhury, T. 1996: Beginning of the continental Jurassic in India: A paleontological approach. In, Morales, M. ed., *Continental Jurassic. Museum of Northern Arizona Bulletin* 60, p 371-378.
- Behrensmeyer, A. K., 1982: Time resolution in fluvial vertebrate assemblage. *Paleobiology*, vol. 8, p.211-227.
- Behrensmeyer, A. K. and Hook, R. S., 1992: Paleoenvironments and taphonomy. In, Behrensmeyer, A. K. *et al. eds.*, *Terrestrial Ecosystem through Time, Evolutionary Paleocology of Terrestrial Plants and Animals*, p. 15-136. The University of Chicago Press, Chicago and London.
- Branson, E. B., 1905: Structure and relationship of American Labyrinthodontidae. *Journal of Geology*, vol. 13, p. 568-610.
- Case, E. C., 1922: New reptiles and stegocephalians from the Upper Triassic of Western Texas. *Carnegie Institution of Washington Publication*, vol. 321, p. 1-84.
- Case, E. C., 1931: Description of a new species of *Buettneria* with a discussion of the brain case. *Contributions from the Museum of Paleontology, University of Michigan*, vol. 3, p. 187-206.
- Case, E. C., 1932: A collection of stegocephalians from Scurry County, Texas. *Contributions from the Museum of Paleontology, University of Michigan*, vol. 4, p. 1-56.
- Chatterjee, S. and Hotton, N. II. 1986: The paleoposition of India.

- Journal of South East Asian Earth Science*, vol. 1, pt. 3, p. 145-189.
- Chatterjee, S., Jain, S. L., Kutty, T. S. and Roychowdhury, T. K., 1987: Mesozoic Gondwana vertebrates of the Pranhita-Godavari valley, Deccan, India—A review. *Geological Survey of India Special Publication*, vol. 11, no.1, p. 195-212.
- Colbert, E. H., 1958: Relationships of the Triassic Maleri Fauna. *Journal of the Palaeontological Society of India*, vol. 3, p. 68-81.
- Colbert, E. H. and Imbrie, J., 1956: Triassic metoposaurid amphibians. *Bulletin of the American Museum of Natural History*, vol. 110, p. 403-452.
- Coldiron, R. W., 1978: *Acroplous vorax* Hotton (Amphibia, Saurerpetontidae) restudied in the light of new material. *American Museum Novitates*, no. 2662, p. 1-27.
- Cope, E. D., 1868: Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Proceedings of the Academy of Natural Sciences, Philadelphia* 1868, p. 208-221.
- Cox, C. B., 1974: Vertebrate paleodistribution pattern and continental drift. *Journal of Biogeography*, vol. 1, p. 75-94.
- Davidow-Henry, B., 1989: Small metoposaurid amphibians from the Triassic of Western North America and their significance. In, Lucas S. G. and Hunt, A. P. eds., *Dawn of the Age of the Dinosaurs in the American Southwest*, p. 278-292. New Mexico Museum of Natural History, Albuquerque.
- DeFauw, S. L., 1989: Temnospondyl amphibians: A new perspective on the last phases in the evolution of the Labyrinthodontia. *Michigan Academician*, vol. 21, p. 7-32.
- Dutuit, J. M., 1976: Introduction à l'étude paléontologique du Trias Continental marocain. Descriptions des premiers stegocephales recueillis dans le Couloir d'Argana (Atlas occidental). *Mémoires du Muséum National d'Histoire Naturelle (Sciences de la Terre)*, Paris, vol. 36, p. 1-253.
- Fraas, E., 1889: Die Labyrinthodonten der Schwabischen Trias. *Palaeontographica*, vol. 36, p. 1-158, pls. 17.
- Fraas, E., 1896: Die schwabischen Triassaurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt. *Mitteilungen des Königl. Naturalien-Cabinet in Stuttgart* 5, p.1-18.
- Fraas, E., 1913: Neue Labyrinthodonten aus der Schwabischen Trias. *Palaeontographica*, vol. 60, p.275-294, pls. 16-22.
- Gregory, J. T., 1980: The otic notch of metoposaurid labyrinthodonts. In, Jacobs, L. L. ed., *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert*, p. 25-136. Museum of Northern Arizona Press, Flagstaff.
- Hay, W. W., Behensky, J. F. Jr., Branson, J. E. and Sloon, J. L. II., 1982: Late Triassic-Liassic paleoclimatology of the proto-central North Atlantic rift system. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 40, p. 13-30.
- Huene, F. von, 1940: The tetrapod fauna of the upper Triassic Maleri beds. *Palaeontologica Indica, New Series*. vol. 32, no. 1, p.1-42, pls. 1-10.
- Hunt, A. P., 1993: Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from Western North America. In, Morales, M. ed., *Aspects of Mesozoic Geology and Paleontology of the Colorado Plateau, Museum of Northern Arizona Bulletin* 59, p. 67-97.
- Hunt, A. P. and Lucas, S. G., 1989: Late Triassic vertebrate localities in New Mexico. In, Lucas, S. G. and Hunt, A. P. eds., *Dawn of the Age of the Dinosaurs in the American Southwest*, p. 72-101. New Mexico Museum of Natural History, Albuquerque.
- Hunt, A. P. and Lucas, S. G., 1991: The *Paleorhinus* biochron and the correlation of the nonmarine Upper Triassic of Pangaea. *Palaeontology*, vol. 34, p. 487-501.
- Jupp, R. and Warren, A. A., 1986: The mandibles of the Triassic temnospondyl amphibians. *Alcheringa*, vol. 10, p. 99-124.
- Kuhn, O., 1932: Labyrinthodonten und Parasuchier aus dem mittleren Keuper von Ebrach in Oberfranken. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Reihe B*, vol. 69, p. 94-144.
- Kutty, T. S., 1971: Two faunal associations from the Maleri Formation of the Pranhita-Godavari valley. *Journal of Geological Society of India*, vol.12, no. 1, p. 63-67.
- Kutty, T. S. and Sengupta, D. P., 1989: Late Triassic formations of the Pranhita-Godavari valley and their vertebrate faunal sequence—a reappraisal. *Indian Journal of Earth Sciences*, vol. 16, no. 4, p. 189-206.
- Long, R. A. and Murry, P. A., 1995. Late Triassic (Carnian and Norian) tetrapods from the Southwestern United States. *New Mexico Museum of Natural History and Science Bulletin* 4, p. 1-254.
- Lucas, S. G., 1998: Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 143, p. 347-384.
- Lucas, S. G. and Hunt, A. P., 1989: Vertebrate biochronology of the Late Triassic. *28th International Geological Congress Abstracts* 2, p. 335-336.
- Lydekker, R., 1885: Maleri and Denwa Reptilia and Amphibia. *Palaeontologia Indica, Series 4*, no.1, p. 1-38.
- Lydekker, R., 1890: *Catalogue of the Fossil Reptilia and Amphibia in the British Museum of Natural History*, Part IV, 296 p. London.
- Maulik, P. and Chaudhuri, A. K., 1983: Trace fossils from continental Triassic red beds of the Gondwana sequence, Pranhita-Godavari valley, South India. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 41, p. 17-34.
- Meyer, H. von., 1842: Labyrinthodonten Genera. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 1842, p. 301-304.
- Miall, L. C., 1875: Report of the committee, consisting of Professor Huxley, L. D., F. R. S.; Professor Harkness, F. R. S.; Henry Woodward, F.R.S.; James Thomson; John Brigg; and L. C. Miall on the structure and classification of the labyrinthodonts. *Report of the Meeting of the British Association for the Advancement of Science*, vol. 44, p. 149-192.
- Milner, A. R., 1990: The radiation of temnospondyl amphibians. In, Taylor P. D. and Larwood G. P. eds., *Major Evolutionary Radiations*, p. 321-349. Clarendon Press, Oxford.
- Milner, A. R., 1994: Late Triassic and Jurassic amphibians, fossil records and phylogeny. In, Fraser, N. and Sues, H.-D. eds., *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, p. 5-22. Cambridge University Press, Cambridge.
- Parrish, J. T., Ziegler, A. M. and Scotose, C. R., 1982: Rainfall pattern and the distribution of coal and evaporites in the Mesozoic and Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 40, p. 67-101.
- Pascoe, E. H., 1959: *A Manual of Geology of India and Burma*, vol II, p. 485-1343. Government of India Press, Calcutta.
- Pye, K., 1983: Red beds. In, Goudie, A. S. and Pye, K. eds., *Chemical Sediments and Geomorphology: Precipitates and Residua in the Near Surface Environment*, p 227-264. Academic Press, London, New York.
- Robinson, P. L., 1970: The Indian Gondwana formations—a review. *1st International Symposium on Gondwana Stratigraphy*, p. 201-268. I.U.G.S. South America.



- Robinson, P. L., 1971: A problem of faunal replacement on Permian-Triassic continents. *Palaentology*, vol. 14, p. 131-153.
- Robinson, P. L., 1973: Paleoclimatology and continental drift. In: Tarling, D. H. and Runcorn, S. K. eds., *Implications of Continental Drift to the Earth Sciences*, p. 451-467. Academic Press, New York.
- Romer, A. S., 1939: An amphibian graveyard. *Scientific Monthly*, vol. 49, p. 337-339.
- Romer, A. S., 1947: Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology Harvard* 99, p. 1-367.
- Roychowdhury, T. K., 1965: A new metoposaurid amphibian from the upper Triassic Maleri Formation of Central India. *Philosophical Transaction of the Royal Society of London, Series B*, no. 250, p. 1-52.
- Sarkar, S., 1988: Petrology of caliche derived calcirudite/calcarenites in the Late Triassic Maleri Formation of the Pranhita-Godavari valley, South India. *Sedimentary Geology*, vol. 55, p. 263-282.
- Sawin, H. J., 1945: Amphibians from the Dockum Triassic of Howard County, Texas. *University of Texas Publication*, no. 4401, p. 361-399.
- Sengupta, D. P., 1990: *New Amphibians (Labyrinthodontia, Temnospondyli) from the Maleri Formation of Deccan, India; their Significance in Geology and Palaeontology*, 152 p. Ph. D. Thesis, (Science, Geology), University of Calcutta.
- Sengupta, D. P., 1992: *Metoposaurus maleriensis* Roychowdhury from the Tiki Formation of the Son-Mahanadi valley of central India. *Indian Journal of Geology*, vol. 64, no. 3, p. 300-305.
- Sengupta, D. P., 1995: Chigutisaurid temnospondyls from the Late Triassic of India and a review of the family Chigutisauridae. *Palaentology*, vol. 38, p. 313-339.
- Sengupta, D. P. and Ghosh, D. P., 1993: Morphometrics of some Triassic temnospondyls. In: Lucas, S. G. and Morales, M. eds., *The Nonmarine Triassic. New Mexico Museum of Natural History and Science Bulletin* 3, p. 423-428.
- Sengupta, S., 1970: Gondwana sediments around Bheemaram, Pranhita-Godavari valley, India. *Journal of Sedimentary Petrology*, vol. 40, p. 140-170.
- Singer, A., 1980: The paleoclimatic significance of clay minerals in soils and weathering profiles. *Earth Science Reviews*, vol. 15, p. 303-326.
- Smith, A. B., 1994: *Systematics and the Fossil Record Documenting Evolutionary Patterns*, 223 p. Blackwell Scientific Publication, Oxford.
- Smith, A. G. and Briden, J. C., 1977: *Mesozoic and Cenozoic Paleontological Maps*, 63 p. Cambridge University Press, London, New York and Melbourne.
- Voorhies, M., 1969: Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska, *University of Wyoming, Contribution to Geology, Special Paper*, no. 1, p. 69.
- Warren, A. A. and Hutchinson, M. N., 1983: The last labyrinthodont? A new brachyopoid (Amphibia, Temnospondyli) from the Early Jurassic Evergreen Formation of Queensland, Australia. *Philosophical Transactions of the Royal Society of London, Series B*, no. 303, p.1-62.
- Warren, A. A. and Snell, N., 1991: The post cranial skeleton of Mesozoic temnospondyl amphibians: a review. *Alcheringa*, vol. 15, p. 43-64.
- Watson, D. M. S., 1919: The structure, evolution and origin of the Amphibia — the orders Rachitomi and Stereospondyli. *Philosophical Transactions of the Royal Society of London, Series B*, no. 209, p.1-73.
- Watson, D. M. S., 1958: A new labyrinthodont (Paracyclotossaurus) from the Upper Trias of New South Wales. *Bulletin of the British Museum of Natural History, London (Geology)*, vol. 3, p. 233-263.
- Watson, D. M. S., 1962: The evolution of the labyrinthodonts. *Philosophical Transactions of the Royal Society of London, ser. B*, no. 245, p. 219-265.
- Welles, S. P. and Cosgriff, J. W., 1965: A revision of the labyrinthodont family Capitosauridae and a description of *Parotosaurus peabodyi*, n. sp. from the Wupatki Member of the Moenkopi Formation of Northern Arizona. *University of California Publications in Geological Sciences*, vol. 54, p. 1-148, pl. 1.
- Werneburg, R., 1990: Metoposaurier (Amphibia) aus dem Unteren Keuper (Obertrias) Thüringens. *Veröffentlichung Naturhistorischen Museum Schleusingen*, vol. 5, no.1, p. 31-38.
- Wilson, J. A., 1941: An interpretation of the skull of *Buettneria* with reference to the cartilages and soft parts. *Contributions from the Museum of Paleontology, University of Michigan* 6, p. 71-111.
- Wilson, J. A., 1948: A small amphibian from the Triassic of Howard County, Texas. *Journal of Paleontology*, vol. 22, no. 3, p. 359-361.
- Zittel, K. A. von., 1888: *Handbuch der Paläontologie Abteilung I. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*, 900 p. R. Oldenbourg, Munich and Leipzig.